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Modelling tools to support the management of crown-of-thorns starfish (Acanthaster cf. solaris) on Australia's Great Barrier Reef

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A thesis submitted for the degree of Doctor of Philosophy

Australian Research Council Centre of Excellence for Coral Reef Studies

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I dedicate this thesis to my father, Ronald Leslie Matthews, who loved me, the ocean and mathematics

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Abstract

Outbreaks of the Pacific crown-of-thorns starfish (COTS; *Acanthaster* cf. *solaris*) have contributed greatly to sustained declines in coral cover on the Great Barrier Reef (GBR) throughout the last 50 years. With the intensity and frequency of bleaching and cyclonic disturbances predicted to increase, effectively managing these outbreaks may give reefs an opportunity to partially recover from these cumulative impacts. Major limitations in contemporary control programs of COTS revolve around understanding of the spatial and temporal patterns of COTS outbreaks. This research addresses these limitations by constructing a spatially explicit COTS-Coral metacommunity model for the GBR between 1996-2017, and building several key modelling tools towards this goal. Firstly, the disturbance history (1985-2017) and abiotic regime were collated for the GBR at a 1x1km resolution as a standardized platform to develop regional scale models for the GBR. To synthesise the extensive and disparate streams of COTS observational data, an interactive visualisation and analytical platform, *The COTS Dashboard* was developed. This tool, currently being used by the Great Barrier Reef Marine Park Authority, allows researchers and managers to assess the severity and extent of COTS outbreaks and monitor progress towards stated management goals. Using the data collated by the two previous tools, a habitat suitability model for COTS was constructed. This model provides the first validated estimates of COTS outbreak probability across the GBR, identifying the importance of a variety of water quality, larval connectivity and abiotic variables in predicting COTS spatial distribution. Finally, a COTS-Coral metacommunity model was built to recreate the trajectories of coral cover and COTS density for the last 23 years accounting for major disturbances, water quality and larval connectivity variability. This model provides a framework within which future management scenarios for COTS outbreaks can be tested. Overall this research aims to provide modelling and data tools for researchers and managers to develop the most effective and efficient management of COTS outbreaks.

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1 General Introduction

1.1 Cumulative disturbances on coral reefs

Coral reefs globally are subject to extensive and sustained degradation (Hughes et al. 2003, Pandolfi et al. 2003, Hoegh-Guldberg et al. 2007, Jackson et al. 2012). Reef degradation began centuries ago with extensive coastal modification and over-exploitation of large and vulnerable species, but has accelerated in recent decades with increasing anthropogenic disturbances and compounding effects of environmental change (Pandolfi et al. 2003, De'ath et al. 2012, Jackson et al. 2012). Moreover, the condition of reef ecosystems is predicted to worsen in coming decades with increasing frequency and severity of dominant stressors (Hoegh-Guldberg 1999, Knutson et al. 2010, Rummukainen 2012, Hoegh-Guldberg et al. 2014, Hughes et al. 2017b). These stressors not only contribute to elevated mortality of habitat-forming organisms (mainly, corals), but undermine the resilience of reef communities. Resilience is defined herein as the capacity of ecological systems to absorb the impact of a disturbance without drastically or permanently deviating from the its initial pre-disturbance state (Hughes et al. 2003, 2010, Folke et al. 2004). Resilience of coral assemblages is eroded by chronic stressors such as ocean warming and acidification, pollution, sedimentation and over-harvesting. Within the context of these chronic stressors, discrete periods of coral loss are most commonly attributed to acute disturbances such as severe tropical cyclones (Wolff et al. 2016), mass coral bleaching (Hughes et al. 2017b), outbreaks of coral disease (Miller et al. 2009b, Bourne et al. 2009) and predation from outbreaks of coral predators such as crown-of-thorns starfish (COTS) *Acanthaster spp* (De'ath et al. 2012, Baird et al. 2013). These disturbances can act independently, but commonly occur in concert with complex interactive effects (Ban et al. 2014, Vercelloni et al. 2017,

MacNeil et al. 2019). For example, on Australia's Great Barrier Reef (GBR) poor water quality increases susceptibility to coral diseases and bleaching (Vega Thurber et al. 2014) and is also hypothesised to contribute to the proliferation of outbreaks of COTS (Fabricius et al. 2010, Brodie et al. 2017). Therefore, it is of vital importance for the future of coral reefs that we better understand the interacting effects of multiple disturbances. Herein, the term "cumulative disturbance" is used to encompass both additive (cumulative) and interactive (synergistic) effects of disturbance on coral reefs.

Given the critical and urgent need for effective and innovative coral reef management (Hughes et al. 2017a, Bellwood et al. 2019), there has been increased focus on understanding the cumulative effect of disturbances and providing modelling frameworks that can adequately simulate their effect on coral cover trajectories (Burke and Reytar 2011, Ortiz et al. 2018, Mellin et al. 2019a). There has been significant development in these fields, such as cumulative impact mapping and assessment (Halpern and Fujita 2013), and the development of frameworks for resilience based management (McCook et al. 2010b, Anthony et al. 2015). However, the modelling frameworks used to determine the effects of multiple disturbances and identify the most resilient reefs are often simply mapping disturbance exposure for reef locations and only account for linear responses of ecosystems to stressors (Hughes et al. 2017a). While these approaches can be useful, temporally explicit modelling frameworks that account for non-linear interactions of multiple stressors are essential. Fundamental to this approach is the collation and standardization of disturbance and environmental data to promote the development of complex regional scale models. Developing such models provides the opportunity to identify important disturbances that may be mitigated and simulate the potential gains (or reduced losses) that may be achievable through a variety of proposed interventions.

Although there are many threats to the future of coral reefs, there are few interventions available for direct action at a local or regional scale that may stall the decline of reefs to allow

reefs to recover from multiple disturbances (Bellwood et al. 2019). Recently, significant effort has been directed towards identifying emerging technologies to promote coral reef restoration, which are aimed to be combined with existing management strategies such as pest and pollution control and no-take areas (van Oppen et al. 2017, Anthony et al. 2017). However, these technologies are in their infancy, while scaling and cost remain significant hurdles. As such, increasing the efficiency of currently available interventions is a key management goal (GBRMPA 2017). Since no management intervention can protect from cyclones, and given that mitigating the impact of climate change requires global coordination, most interventions on the GBR have been directed towards improving water quality (Kroon et al. 2016), creating marine reserves (McCook et al. 2010a) or the manual removal of the dominant coral predator, COTS (Westcott et al. 2016, Pratchett and Cumming 2019). The remainder of this introduction will focus upon the causes, consequences and management of COTS in the broader context of cumulative disturbances to coral reefs. Importantly the following sections will highlight key areas in which modelling tools can contribute to the improved management of COTS outbreaks with the ultimate goal of enhancing the condition and resilience of coral-dominated habitats.

1.2 Outbreaks of crown-of-thorns starfish (COTS)

Outbreaks of the coral-eating crown-of-thorns starfish (COTS, *Acanthaster* spp.*)* represent one of the most significant causes of coral loss throughout the Indo-Pacific (De'ath et al. 2012, Baird et al. 2013). During outbreaks, densities of COTS may reach 151,650 starfish km^{-1} (Kayal et al. 2012). The combined feeding activity of high densities of large COTS cause extensive and widespread coral loss (Chesher 1969, Kayal et al. 2012). Given that corals are essential for maintaining productivity and biodiversity in reef ecosystems (Holbrook et al. 2000, Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2008), COTS outbreaks directly contribute to the degradation of coral reef ecosystems, jeopardising ecosystem function and fisheries production. On Australia's Great Barrier Reef (GBR), there have been four

documented outbreaks of the Pacific species of COTS (*Acanthaster* cf. *solaris*) since the 1960's, contributing to significant and sustained declines in coral cover (Pratchett et al. 2014). Since 1982, the average coral cover at reefs monitored by the Long Term Monitoring Program (LTMP) of the Australian Institute of Marine Science has declined by 50% and nearly half of this loss was attributed to successive outbreaks of COTS (De'ath et al. 2012). Unlike other causes of coral loss (e.g., tropical cyclones, coral bleaching and disease), outbreaks of COTS may be amenable to direct action (Pratchett et al. 2014). Consequently, management strategies such as increasing the efficiency of direct control (Rivera-Posada et al. 2014, Fletcher and Westcott 2016, Doyle et al. 2017), developing biological controls (Endean 1969, Hall et al. 2017a), or addressing the anthropogenic disturbances that may initiate or exacerbate outbreaks (Kenchington and Kelleher 1992, Brodie and Waterhouse 2012) are the most promising direct approaches to halt or reverse declining coral cover on the GBR (Pratchett et al. 2014). However, in order to predict and subsequently prevent the spread of future outbreaks and thus protect the remaining live coral on the GBR, it is essential to understand the mechanisms driving these outbreaks.

Outbreaks of COTS are generally defined as starfish > 1,500 individuals km^{-2} (15 individuals ha^{-1} or 0.22 per 2 min manta-tow), which was estimated as the maximum sustainable density of starfish for a reef with average coral cover (Moran and De'ath 1992, Pratchett et al. 2014). More recent calibration however, has adjusted these thresholds due to lower than previously assumed detectability of manta tow to be >4,900 individuals km^{-2} (49 individuals ha^{-1} or 0.22 per 2 min manta-tow) (De'ath 2003). One major school of thought suggests that outbreaks are initiated as a result of gradual accumulation of individuals from successive recruitment events, known as "primary outbreaks" (Endean 1974, Johnson 1992, Stump 1996, Pratchett 2005a). Once these primary outbreaks have established, the increased density of adult starfish overcome Allee thresholds and fertilisation is dramatically increased (Rogers et al. 2017). With

the combination of increased fertilisation rates and the immense fecundity of the species (Conand, 1984; Kettle & Lucas, 1987) it is almost inevitable that the dramatic increase in offspring production from a primary outbreak give rise to a wave of "secondary outbreaks" that propagate southwards along the GBR (Endean 1974, Reichelt et al. 1990a). Secondary outbreaks are a logical consequence of large established breeding populations (Pratchett et al. 2014), and are expected to propagate across the GBR in accordance with predominant hydrodynamic flows (Dight et al. 1990a, 1990b, Hock et al. 2014, Thomas et al. 2014).

Hypotheses accounting for the initiation of outbreaks have largely been concerned with factors affecting larval survival (e.g. 'terrestrial-runoff hypothesis' (Birkeland 1982)), or post-settlement survival (e.g. 'predator removal hypothesis' (Endean 1969); 'prey-threshold hypothesis' (Antonelli and Kazarinoff 1984)). However, single factor hypotheses oversimplify the complex dynamics of COTS outbreaks (Babcock et al. 2016a) and overlook the predisposition of this organism to major fluctuations in abundance due to their immense fecundity (Conand 1984, Kettle and Lucas 1987), combined with the capacity for synchronous spawning and fertilisation over large distances (Babcock and Mundy 1992, Benzie 1992). Moreover, increased eutrophication (from terrestrial runoff) may promote increased larval survival, allowing the high reproductive capacity of COTS (Babcock et al. 2016b) to be translated to recruitment success. The terrestrial run-off hypothesis (first proposed by Birkeland 1982) has been further supported by experimental studies showing that increased phytoplankton concentrations (using chlorophyll-a as a proxy) lead to significant increases in rates of larval development and survivorship (Fabricius et al. 2010, Wolfe et al. 2015, 2017, Pratchett et al. 2017b). Periods of optimal Chl-a concentrations for larval survival (1 µg chl-a L^{-1}) are natural background conditions for some inner shelf reefs and represent peak eutrophic conditions following storms and floods in the mid and outer-shelf reefs (Wolfe et al. 2015). Woolridge and Brodie (2015) suggested that primary outbreaks are initiated by the

combination of increased Chl-a concentrations and increased larval retention as a result of neutral ENSO conditions in the north-Central GBR (Cairns-Lizard Island), an area referred to as the "initiation box". This claim is supported by recent larval connectivity models which highlight the formation of isolated clusters at small dispersal distances (<27km) (Kininmonth et al. 2010) and also elevated short and long-range connectivity within the "initiation" box (Hock et al. 2017).

The focus of much COTS research on the "terrestrial run-off hypothesis" and extensions thereof, whilst providing significant advances to understanding larval survival, has diminished the emphasis on developing a more holistic explanation of COTS outbreaks (Pratchett and Cumming 2019). The causes of COTS outbreaks are complex and synergistic, requiring the alignment of environmental, hydrodynamic and demographic conditions and this complexity should be reflected by research priorities. There also remains a significant lack of empirical data on some key-life history demographics (e.g. fecundity, fertilisation success, spawning, and settlement cues). For our understanding to advance, it is therefore imperative to synthesise the extensive time-series field observations of COTS outbreaks with the increasingly accurate estimates of environmental thresholds (e.g., Chl-a and temperature), hydrodynamic modelling and increasingly available information regarding environmental conditions across the GBR. Synthesising these currently disparate aspects of COTS research into a single modelling framework may allow for the forecasting and early detection of COTS outbreaks, and ultimately the development of more effective mitigation strategies.

1.3 Modelling COTS Outbreaks

Increasingly, complex ecological models are being developed to understand species invasions and outbreaks of pest species (Elith et al. 2010, De Rivera et al. 2011, Václavík and Meentemeyer 2012, Cockrell and Sorte 2013, Mellin et al. 2016b). Below I outline four key,

generally independent modelling procedures of increasing complexity used to model range expanding species and show how each can act as a building block for a fifth; metapopulation modelling framework that will both generate predictions for management of the COTS problem and provide a novel template for modelling range-expanding marine species modelling.

1.3.1 Species Distribution Modelling (SDM)

Species distribution models (i.e. SDM; a.k.a. ecological niche or habitat suitability models) describe or predict the probability of presence of a species, or patterns of its abundance, across environmental gradients or in a specific geographical area (Pearman et al. 2008, Peterson et al. 2011). SDM is essentially a correlative technique that fits a statistical relationship between observations and predictor variables (usually environmental conditions). Such models can be useful as a first step towards identifying newly suitable habitats. For example, in response to warming temperatures, invasive species could expand once dispersal barriers are breached (De Rivera et al. 2011, Araújo and Peterson 2012, Jones et al. 2013). SDM only require geographically referenced presence/absence/abundance observations and associated environmental data to derive predicted distributions. These models are constrained by the underlying assumption that species occurrences accurately portray the range of suitable environments that the species is at equilibrium with (Thuiller 2005, Elith et al. 2010, Václavík and Meentemeyer 2012). This assumption, however, is often violated for range-expanding species as their range changes over time (Elith et al. 2010). Additionally, many SDMs rely solely on presence data as true absence data are missing and thus an assumed pseudo-absence matrix must be generated (Graham et al. 2004, Ferrier and Guisan 2006). For COTS however, these limitations are somewhat alleviated by the fact that outbreaks occur within their native range and that both presence and absence data are available. Although substantial observational and environmental data exists, there has not yet been an attempt to model COTS spatial distribution and determine its drivers.

1.3.2 Biophysical/Mechanistic Modelling

Mechanistic models (a.k.a. biophysical models) rely on species physiological tolerance limits and, in doing so, enable the modelling of species distributions across environmental gradients without using species distributions per se (Kearney and Porter 2009). Biophysical models tend to yield more robust predictions than SDM because they explicitly account for the relationships between environmental conditions and organismal performance, irrespective of a species' current distribution that can sometimes misrepresent its potential range due to e.g. depletion from harvesting (Buckley et al. 2010). Therefore, biophysical models are particularly useful when a species' distribution is not at equilibrium, or determined by a particular physiological response (Buckley et al. 2010). Such biophysical models are increasingly used to model range dynamics in response to climate change (Kearney et al. 2010, Cheung et al. 2011) or seasonal temperature gradients (Monahan 2009), and the use of such models is particularly promising when data are sufficient to couple them with SDMs to improve predictions (Elith et al. 2010, Fordham et al. 2013). As mentioned previously, the extensive work done on COTS larval development and survivorship offers the opportunity to create a coupled mechanistic-SDM that could overcome some of the difficulties associated with modelling outbreaking species.

1.3.3 Larval Connectivity Modelling

Larval dispersal/connectivity models are built upon underlying hydrodynamic models/empirical data for a given area, and can be interrogated to determine probabilities of larval dispersal between nodes of a network (Condie et al. 2012, Thomas et al. 2014, Hock et al. 2017). The advantage of this approach is that it explicitly deals with the potential for external sources and sinks, and they are particularly useful for modelling invertebrate species where populations are easily surveyed and migration is largely limited to a pelagic larval stage (Robinson et al. 2011). Larval connectivity models were first developed for COTS on the GBR in the late 1980s (Dight et al. 1990a, 1990b), however, recent advances in high resolution

hydrodynamic modelling in the GBR (Herzfeld & Waring, 2006; Condie et al., 2012; Thomas et al., 2014) has increased the feasibility of accurately modelling dispersal events within this complex system. Indeed, some network analyses have already confirmed the importance of the "initiation box" as a source of larvae for downstream outbreaks, and have been used to predict the likelihood of outbreaks (Hock et al. 2014, 2017). These efforts, however, do not take into account habitat suitability for COTS, and are built solely upon the maximum potential larval connectivity between reefs. An important extension of these models is to incorporate the extensive COTS observation and environmental data to predict reefs most likely to experience COTS outbreaks and to validate these predictions

1.3.4 Demographic Population Modelling

Demographic models that explicitly account for species vital rates (e.g. births, mortality, fecundity) and stage-specific growth rates are being increasingly used to model invasive or outbreaking species (Fordham et al. 2013). Demographic models overcome some limitations of SDM as they can incorporate dispersal as well as vital rates that can vary over space and time (Mellin et al. 2016b). Demographic models can be either population-based, accounting for population-level parameters such as survival and fertility rates and dispersal kernels, or individual-based, accounting for individual parameters such as body size, sex, behaviour (Mellin et al. 2016). For COTS some studies have developed age-structured population models, however they generally estimate vital rates from the model (Mccallum 1990, Morello et al. 2014), even though there are data available on growth rates of juvenile and adult COTS (Lucas 1984, Caballes and Pratchett 2014, Wilmes et al. 2016), as well as size-dependent fecundity (Kettle and Lucas 1987, Babcock et al. 2016b). These studies provide a solid foundation for further developing stage based demographic models, with a number of independent (and calibrated) datasets (MacNeil et al. 2016) available for use in the validation process. Most importantly however, recent advances in the development and usage of statistical software

(such as R) allow the synthesis of other important factors for invasive species such as landscape dynamics, habitat suitability and dispersal/connectivity into a spatially explicit metapopulation framework (Lurgi et al. 2015).

1.3.5 Metapopulation and Metacommunity Modelling

A metapopulation is a "population of populations" (Levins 1969), a set of individual populations linked by source-sink dynamics (as estimated through larval connectivity modelling) and separated by unsuitable habitat (species distribution modelling). A metacommunity model, however represents a set of set of local communities that are linked by dispersal (Holyoak et al. 2005). A metacommunity model for COTS therefore, coalesces the outputs of the aforementioned modelling techniques with spatially explicit coral growth and disturbance to provide predictions representing a more comprehensive explanation of the complex ecological relationships than is possible using other methodologies. Metapopulation models have already been developed for COTS (Mccallum 1990, Scandol 1999), but do not account for spatially explicit coral growth, disturbance and recovery as in a metacommunity framework and were built using low-resolution hydrodynamic models that cannot accurately recreate near-shore processes. Condie et al. (2018) advanced these approaches by incorporating coral growth and recovery from cumulative disturbances and management simulations, however this approach is currently not spatially explicit. Recent advances in both larval connectivity modelling on the GBR (Condie et al. 2012, Hock et al. 2014) as well as the development of disturbance datasets (Matthews et al. 2019) and coral growth models (MacNeil et al. 2019, Mellin et al. 2019a), allow for a more accurate spatially explicit metacommunity model to be developed for COTS on the GBR.

1.3.6 Crown-of-thorns modelling

Previous modelling studies have tackled the COTS problem with varying levels of detail, drawing from a vast range of empirical and simulated data. However, there has not yet been any attempt to combine all of the best available data into a modelling framework that takes advantage of the computational and statistical advances of the last decade. Metapopulation models created in the 1990's (Scandol and James 1992, Scandol 1999) were underpinned by the hydrodynamic models of Dight et al. (1990a), which have now been surpassed in spatial resolution (~10km vs ~0.25-4km) (Herzfeld and Waring 2006, Condie et al. 2012, Thomas et al. 2014). Furthermore, due to computational limitations, a number of important biological processes (namely coral growth and recovery after an outbreak) were oversimplified within these models. Morello et al. (2014) developed a model which incorporated trophic interactions as a mechanism for controlling COTS populations, focusing on the empirical data from Lizard Island. Aside from its limited spatial extent, this model only successfully recreated historical outbreaks when recruitment rates were artificially manipulated. The initiation of outbreaks within the "initiation box" was modelled mechanistically by Wooldridge and Brodie (2015) who combined simulated nutrient loads and hydrodynamic connectivity with empirical historical records of COTS outbreaks to highlight the coincidence of outbreaks following peak nutrient loading on strong local clustering of reefs during neutral ENSO conditions. This mechanistic approach, whilst explaining convincingly the initiation mechanism does not provide a framework to simulate COTS outbreak probabilities under a variety of scenarios or determine best management practices to control these outbreaks. There is a need to develop a metacommunity model framework that will combine the most up to date empirical and simulated data, building upon knowledge gained from recent mechanistic (Wooldridge and Brodie 2015), connectivity (Hock et al. 2014) demographic (Morello et al. 2014) and metacommunity models using simulated reef locations (Condie et al. 2018). This framework should extend the temporal and spatial scope of recent models whilst incorporating relevant

biological processes with finer spatial resolution to provide the most accurate information to managers of COTS outbreaks.

1.4 Management of COTS on the Great Barrier Reef

Widespread support for management intervention followed the first global reports of COTS outbreaks (Westcott et al. 2016) such as in the Ryukyu Archipelago in Japan in 1957 (Yamaguchi 1986), in Guam (1967) and Palau (1969) and on the GBR near Green Island in 1962 (Endean 1969, 1982). Although the question of whether COTS outbreaks represent a natural phenomenon remains largely unresolved (Dana and Wolfson 1970, Vine 1973, Uthicke et al. 2009, Pratchett et al. 2017a), the priority for managers has transformed into whether the threat to corals and in particular the GBR are sufficient to elicit direct intervention (Westcott et al. 2016). Indeed, most research throughout the 1980's and 1990's focused on the organism itself, and the processes underpinning outbreaks. While the efficacy of control efforts and best practices remain in doubt (Pratchett et al. 2017a, Pratchett and Cumming 2019), recent understanding of the interactions between COTS and other disturbances to coral reefs (Vercelloni et al. 2017, Ortiz et al. 2018, MacNeil et al. 2019, Mellin et al. 2019a), have highlighted the urgency of action. While tropical cyclones, bleaching events, outbreaks of COTS, and poor water quality act cumulatively to reduce coral cover, it is outbreaks of COTS that are most amenable to direct management actions at the reef scale (Pratchett et al. 2014).

Control programs of COTS began as early as 1962 on the GBR, in an immediate response to the first documented outbreak at Green Island. Despite the initial success observed, control programs were soon overwhelmed, presumably from increasing propagule pressure from outbreaks on surrounding yet unmonitored reefs (Kenchington 1978). Initial failures and ineffective time intensive control methodologies (cut up in situ, removed and buried onshore) led to the widespread belief that COTS control was best focused on small sites with tourism value (Walsh et al. 1971, Westcott et al. 2016). However in recent years the development of single-shot lethal injections using bile salts (Rivera-Posada et al. 2011, 2014) and more recently household vinegar (Boström-Einarsson and Rivera-Posada 2016), has dramatically improved

the effectiveness of manual control (Pratchett et al. 2018), increasing the potential for an effective control program.

Following the development of the lethal injection there has been a concerted effort to improve the strategic allocation of COTS control resources (Fletcher and Westcott 2016, Westcott et al. 2016). The Great Barrier Reef Marine Park Authority (GBRMPA) began funding a dedicated COTS Control Program from 2012, operating 1-2 vessels and focused mostly on reefs with high tourism value between Lizard Island and Cairns (GBRMPA 2018a). However, the development of an integrated pest management approach to COTS control has aimed to increase the strategic allocation of current and increasing effort for the benefit of the entire reef ecosystem (Fletcher and Westcott 2016). With increased funding from 2018 to support five vessels across a greater extent of the GBR, a greater impetus has been put on identifying reefs where COTS control may have the greatest regional impact (Fletcher and Westcott 2016, GBRMPA 2017). Larval connectivity models developed for both COTS and corals have aimed to identify reefs that are disproportionately responsible for the spread of secondary outbreaks, and those which may effectively spread coral larvae and promote recovery and resilience at a regional scale (Hock et al. 2014, 2016, 2017). The combination of improved manual control technologies, combined with the development and implementation of reef-level and regional-level strategic planning has reinvigorated the research and management communities to attempt broad scale COTS control in a bid to buy more time for coral reefs on the GBR.

Alongside improvements to the contemporary control techniques for COTS, a number of emerging technologies may prove pivotal in the early detection and increased efficiency of control in the next wave of outbreaks. Foremost of these advances has been the development of eDNA larval detection methods to identify the presence of COTS larvae in seawater samples (Doyle et al. 2017). While initial trials were restricted to indicating simply a presence or absence, there is scope that this technology may be able provide a relative estimate of larval abundance (Uthicke et al. 2018). Clearly, methods such as these provide a realistic opportunity to identify the build-up of COTS preceding a primary outbreak and thus trigger the ramping up of manual control activities, to attempt to suppress or limit the spread of secondary outbreaks.

Additionally, larval monitoring could be conducted on reefs identified as important source reefs to allow the COTS control program to divert control resources in an effort to quickly suppress secondary outbreaks on disproportionately important reefs within the network. Furthermore, automated underwater vehicles (Dayoub et al. 2015, Llewellyn and Bainbridge 2015) may be used to provide more extensive monitoring for COTS (and potentially larvae) augmenting the capabilities of the control program fleet. Another potentially important development is the identification of COTS pheromones involved in both predator response cues and aggregatory behaviour (Beach et al. 1975, Miller 1989, Hall et al. 2017a, 2017b). In the context of COTS control, predator alarm cues could potentially be spread across a reef to disrupt spawning and feeding behaviour, while aggregation cues could be used to essentially create a 'trap' for COTS, further increasing the efficiency of manual control, particularly for the more cryptic sub-adult life stages of COTS.

Although significant progress has been made in understanding and managing COTS outbreaks, especially on the GBR (Pratchett et al. 2017a), there is room for improvement, particularly with regards to the analysis and simulation of COTS populations over space and time. Primarily there is a need for the development of datasets that collate existing disturbance history and environmental variables, to provide a platform to model COTS outbreaks within the broader context of cumulative disturbances on the GBR. Secondly, extensive ecological data have been collected by the COTS control program and various organisations, and there is a need for tools that synthesises and help visualize these data. Such tools could provide managers with more timely feedback on the severity and extent of COTS outbreaks across the GBR and provide essential information on the progress towards stated management goals and the implementation of the integrated pest management process. Thirdly, while there have been many hypotheses put forward to explain the initiation and spread of COTS outbreaks, there has yet to be a study that compares the relative support of these hypotheses using empirical data and provide predictions of unmonitored reefs most likely to experience COTS outbreaks. Finally, with the focus of COTS control shifting towards the next major outbreak, and the emergence of new technologies to help control efforts, modelling frameworks that can simulate the initiation and

spread of COTS populations are needed to prioritise control efforts for the next wave of COTS outbreaks.

1.5 Thesis Outline

The overarching aim of this thesis is to develop effective modelling and management tools to aid in the efforts to control (or contain) COTS populations, and thereby improve the resilience of coral populations on the GBR. Research is developing rapidly with regards to both the understanding of COTS biology and behaviour, but also methods with which to more accurately model populations of COTS. While numerous studies have attempted to explain the causes and consequences of COTS outbreaks on the GBR, there still has yet to be developed a modelling approach that incorporates many of the contributing factors in a temporally and spatially explicit manner and places it within the context of cumulative disturbances. This thesis aims to build the modelling platform in which to achieve these goals through creation of a COTS-Coral metapopulation model for the GBR and documents the independent tools created along the way to aid in the effective management of COTS on the GBR.

Chapter 2 collates existing datasets to create a near complete disturbance history and abiotic characterization for reef locations across the GBR. The reasoning behind this chapter is to provide a standardized framework upon which more complex regional scale models can be developed to limit the recreation of similar datasets by different groups of scientists. Most importantly, Chapter two promotes the building of models that account for cumulative disturbances across time and space, whilst being placed in the broader context of a reef's abiotic environment. This data collection provides annual estimates between 1985-2017 for exposure to damaging cyclonic waves (Puotinen et al. 2016), exposure to thermal stress (Degree Heating Weeks, https://coralreefwatch.noaa.gov/satellite/bleaching5km/index.php), interpolated estimates of COTS density (Sweatman et al. 2008) and bleaching severity from three major bleaching events on the GBR (1998, 2002, 2016) (Berkelmans et al. 2004, Hughes et al. 2018b). Additionally, the dataset includes a mean and seasonal range estimates for environmental variables (Huang et al. 2013) as well as satellite derived relative exposure to flood plumes as a

useful proxy indicators of water quality (Devlin et al. 2012a, Alvarez-Romero et al. 2013). This chapter provides the foundation for modelling described in Chapters 4-6 and provides reef researchers with a standardised approach to building regional scale models for the GBR, which has already been implemented by recent modelling of coral growth disturbance and resilience on the GBR (MacNeil et al. 2019, Mellin et al. 2019).

Chapter 3 develops a data synthesis and visualisation platform, essential to the expanding COTS control and monitoring activities. This data tool is built within the rapidly developing Business Intelligence (BI) software Power BI, and aims to leverage the advances of business software for conservation purposes. Specifically, *The COTS Dashboard* provides reef managers with up-to-date information regarding the severity and extent of COTS outbreaks across the GBR, progress towards reaching management goals on reefs prioritised for action and information on how integrated pest management practices are being implemented. As the COTS Control program has expanded 3-fold since 2018, synthesis tools such as this are integral for the COTS control program to embed data-driven decision making into each stage of the process. More broadly, the COTS Dashboard provides an example of the utility of applying powerful BI software to synthesise complex spatial and temporal data. This approach has the potential to be applied in much broader conservation contexts, as part of a well-developed adaptive management strategy.

Chapter 4 aims to create a species distribution model for COTS in order to both evaluate the relative support given to competing hypotheses for the spatial distribution of COTS and create the first validated reef level predictions for outbreak probability. This Chapter uses the disturbance and environmental dataset developed in Chapter 2 as candidate predictor variables and the COTS observation data synthesised in Chapter 3 as response variables. Models of species distribution are built using both boosted regression trees (De'ath 2007, Elith et al. 2008) and generalised additive models (Fisher et al. 2018) to identify the most influential predictors of COTS distributions. Importantly, a number of variables are derived from larval connectivity networks, and used to account for spatial autocorrelation, making predictions more closely linked to the oceanographic processes that drive COTS spatial distribution (Hock et al. 2014).

Predictions are validated against independent data collected by the Australian Institute of Marine Science's Long Term Monitoring Program (AIMS LTMP) (Sweatman et al. 2008), providing the first GBR predictions of COTS spatial distribution. Importantly, these models are a useful platform for COTS management that could be automated to leverage the extensive observation data being collected by the COTS Control Program and provide up-to-date predictions of COTS distributions for additional locations that have not been explicitly surveyed. This approach could help refine prioritisation procedures by filling in gaps regarding the current distribution of COTS across the GBR.

Chapter 5 investigates the spatial resilience of coral populations across the GBR by developing a spatially explicit model of coral growth and disturbance, built upon the same 1x1km grid used in Chapter 2. This chapter builds upon MacNeil et al's (2019) Gompertz based model of coral growth and disturbance that was derived for 47 reefs across the GBR monitored by the AIMS LTMP. This model estimates growth rates for each of these reefs and the effect size of each disturbance (cyclones, bleaching, disease, COTS). This chapter uses multivariate regression trees to characterise the benthic community type for each of the sampled locations using the abiotic component of the data collated in Chapter 2 and then predicts out to unsampled locations. Similarly, the initial (1996) and maximal coral cover for each surveyed reef is modelled using a boosted regression tree approach to define the environmental drivers of these two variables, before predicting out to the rest of the GBR. A yearly coral growth model was then calibrated to AIMS LTMP data using the disturbance history collated in Chapter 2 to recreate the trajectory of coral cover across the GBR between 1996-2017 at a 1x1km resolution. This model identifies both the major causes of coral decline and regions of the reef that have to date been the most resilient to disturbance. Importantly this model provides a foundation upon which to build a COTS-Coral metapopulation model to simulate the initiation and spread of COTS populations in order to simulate a range of potential interventions.

Chapter 6 builds upon the knowledge and modelling frameworks developed in the preceding chapters to develop a spatially explicit metacommunity model for COTS-Coral across the GBR. This model aims to incorporate the extensive research that has gone into understanding

COTS outbreaks (Pratchett et al. 2014, 2017a). This stage-based model explicitly models larval survival rates based on nutrient conditions estimated across the GBR (CSIRO 2019), larval dispersal via estimated connectivity networks (Hock et al. 2017) and fertilisation by density and Allee effects (Rogers et al. 2017). Importantly ratio-dependent mortality and fecundity responses are used to incorporate important biotic interactions between COTS and their coral prey (Mellin et al. 2016b). This model was validated against the extensive AIMS LTMP dataset, and provides independent estimates of uncertainty for each reef sector and cross shelf location. Importantly, once calibrated, this model provides a platform for simulating a variety of COTS control strategies proposed for the next outbreak cycle and investigating their potential effects. This model will prove a useful tool for COTS management to help allocate the strategic deployment of limited resources in both the current outbreak and future outbreaks.

Chapter 7 is a general discussion, providing an overview of the major finding of the thesis. This chapter evaluates the significance and management implications of this research and highlights key further research to be undertaken to further improve the understanding of COTS outbreaks and refine best management practices.

Finally, three publications are attached as appendices to this thesis. These publications represent additional research related to COTS outbreaks and coral growth modelling in which I was involved during the course of my PhD. Appendix 1 focuses on modelling growth rates of COTS juveniles, for which I helped develop and analyse the models and reviewing drafts of the paper. Appendix 2 focuses on the theoretical importance of including biotic interactions when modelling species distributions using COTS-Coral as the case study. For this article, I helped synthesise literature for the framing of the research as well as reviewing drafts for submission. Finally, Appendix 3 developed the coral growth model which was used to further develop the Coral-COTS metacommunity model of Chapters 5 and 6. My contribution to this research was to collate the disturbance data and environmental data necessary to estimate effect sizes of different disturbances and to review drafts of the publication.

2 High-resolution characterization of the abiotic environment and disturbance regimes on the Great Barrier Reef, 1985–2017

2.1 Abstract

This data compilation synthesizes 36 static environmental and spatial variables, and temporally explicit modelled estimates of three major disturbances to coral cover on the Great Barrier Reef (GBR): (i) coral bleaching, (ii) tropical cyclones, and (iii) outbreaks of the coral-eating crown-of-thorns starfish, *Acanthaster* cf. *solaris*. Data are provided on a standardized grid (0.01° × 0.01° ~ 1km × 1km) for reef locations along the GBR, containing 15,928 pixels and excluding the northernmost sections (< 12°S) where empirical data were sparse. This compilation provides a consistent and high-resolution characterisation of the abiotic environment and disturbance regimes for GBR reef locations at a fine spatial scale to be used in the development of complex ecosystem models. Static estimates of environmental variables (e.g. depth, bed shear stress, average temperature, temperature variation) originally developed by the Commonwealth of Australia's Environment Research Facility (CERF) Marine Biodiversity Hub (http://www.marinehub.org/) were provided by Geoscience Australia (Huang et al. 2010). Annual (1985-2017) disturbance estimates were either interpolated from empirical data (*A.* cf. *solaris*), predicted from proxy indicators (e.g. Degree Heating Weeks (DHW) as a proxy for bleaching severity), or explicitly modelled (e.g. wave height model for each cyclone). This dataset synthesizes some of the most recent advances in remote sensing and modelling of environmental conditions on the GBR; yet it is not exhaustive and we highlight areas that should be expanded through future research. The characterization of abiotic and disturbance regimes presented here represent an essential tool for the development of complex regional

scale models of the GBR; preventing redundancy between working groups and promoting collaboration, innovation and consistency.

2.2 Introduction

Over the past three decades, coral cover on the GBR has been steadily declining (Sweatman et al. 2011, De'ath et al. 2012) and there is a need to understand (i) when and where reefs have been affected by disturbance; (ii) the magnitude of these disturbances; and (iii) how reefs are likely to respond to future disturbance. Although there has been extensive long-term monitoring of the GBR since 1983 (Sweatman et al. 2008), the sheer scale of the GBR, with ~3,000 individual reefs stretching ~2,300km (GBRMPA 2018b), renders comprehensive reef monitoring impossible. It is therefore imperative that researchers develop data tools and models to fill in the gaps to augment our understanding of the system, by incorporating large datasets into complex yet realistic models. There have been significant developments of regional-scale models for the GBR, especially in terms of hydrodynamic modelling providing estimates of larval connectivity (Condie et al. 2012, Hock et al. 2014) and a vast array of bio-geophysical parameters (Chen et al. 2011, CSIRO 2019). There have also been a number of studies characterizing disturbance regimes on the GBR (De'ath et al. 2012, Maynard et al. 2016), yet these are yet to be consolidated into a dataset and made accessible to reef researchers in a truly transparent manner, promoting consistency among the multiple ecosystem models developed at a regional scale. The lack of such data repository currently represents a significant obstacle for the advancement of ecological modelling and innovative conservation planning, which are of increasing importance due to the predicted impacts of climate change on the GBR (Van Hooidonk et al. 2016, Wolff et al. 2018).

Here, we provide a compilation of static environmental and spatial variables as well as annual disturbance layers on the same 0.01°-resolution grid across the GBR. These variables have been used successfully to predict fish diversity (Mellin et al. 2010a) and spatial turnover (Mellin et al. 2014), and other inter-reef species richness and abundance on the GBR (Sutcliffe et al. 2014). These data were also used to assess the potential for model transferability to predict

species richness in data-poor locations (Sequeira et al. 2016). These studies highlight the utility of these types of environmental and relative spatial variables as proxy indicators for complex, and difficult to estimate, environmental processes. Such datasets allow researchers to extrapolate diversity patterns and thereby gain statistical and ecological insight into complex and large-scale ecological systems that until recently could only be analysed theoretically or through comprehensive sampling.

In addition to static environmental and spatial variables, this dataset provides annual layers of disturbance severity for three major sources of disturbance on the GBR, namely (i) coral bleaching, (ii) tropical cyclones, and (iii) outbreaks of the coral-eating *A.* cf. *solaris.* The disturbance layers are presented on the same 0.01°-resolution grid and summarise the annual exposure to each type of disturbance. Heat stress exposure, linked to coral bleaching, is modelled from satellite data using the established Degree Heating Week metric (DHW) (Eakin et al. 2010, Liu et al. 2014, 2017), and complemented with interpolated values from previously-published aerial bleaching surveys (Berkelmans et al. 2004). Whilst exposure to cyclone activity is to some extent captured by the static variable as cyclone induced bed sheer stress (Table S 9.2; GMCS_STRESS), explicit annual estimates of cyclone exposure are also included in this dataset. Annual cyclone exposure is modelled as cumulative hours exposed to potentially damaging waves (>4m) generated by tropical cyclones (Puotinen et al. 2016). Finally, densities of *A.* cf. *solaris*, originally recorded as number of individuals per sampling unit (manta tow) are drawn from the extensive Long Term Monitoring Program (LTMP) of the Australian Institute of Marine Science (AIMS) (Sweatman et al. 2008). These temporally and spatially explicit disturbance data are designed to be used either alone or in conjunction with the environmental and spatial variables, to understand complex ecological problems such as distribution patterns, benthic community assemblages, bioregional classification and predicting growth and recovery rates of coral communities.

While the main objective of this dataset is for environmental, spatial and disturbance data to be more readily available and user-friendly for marine ecologists and managers, it is also useful to highlight knowledge gaps, such as our limited understanding of *A.* cf. *solaris* population

densities in time and space (MacNeil et al. 2016). This will guide future research and encourage contributions to the expansion and/or improvement of this dataset. Furthermore, it provides a temporal benchmark against which future progress or alternative models of disturbance estimates can be compared and improved upon. The release of this dataset aims to motivate further and more standardised implementation of regional-scale models of complex ecological processes on the GBR.

2.3 Data Collation Methods

Environmental and disturbance data were compiled for all inshore, mid-shelf and outer reefs along much of the length of the GBR, excluding the northernmost sections (< 12°S) where empirical data were sparse. The GBR was split into a total of 15,928 grid cells of 0.01° resolution (Figure S2) that contained reef habitats. The bioregion classification made by the Great Barrier Reef Marine Park Authority (GBRMPA), the cross-shelf location (inner, middle or outer shelf), and latitudinal sector defined by the Australian Institute of Marine Science's (AIMS) Long Term Monitoring Program (LTMP) were identified for each grid cell (Figure 2.1).

Environmental data were obtained from the Commonwealth of Australia's Environment Research Facility (CERF) Marine Biodiversity Hub (http://www.marinehub.org/). Disturbance data were sampled from satellite data and aerial surveys (Bleaching), modelled from storm wave models (Cyclones) or interpolated from empirical observations (*A.* cf. *solaris*). Environmental variables are given as a single static estimate (i.e. long-term average), whilst yearly estimates of disturbance exposure (1985-2017) are presented for the three sources of disturbances.

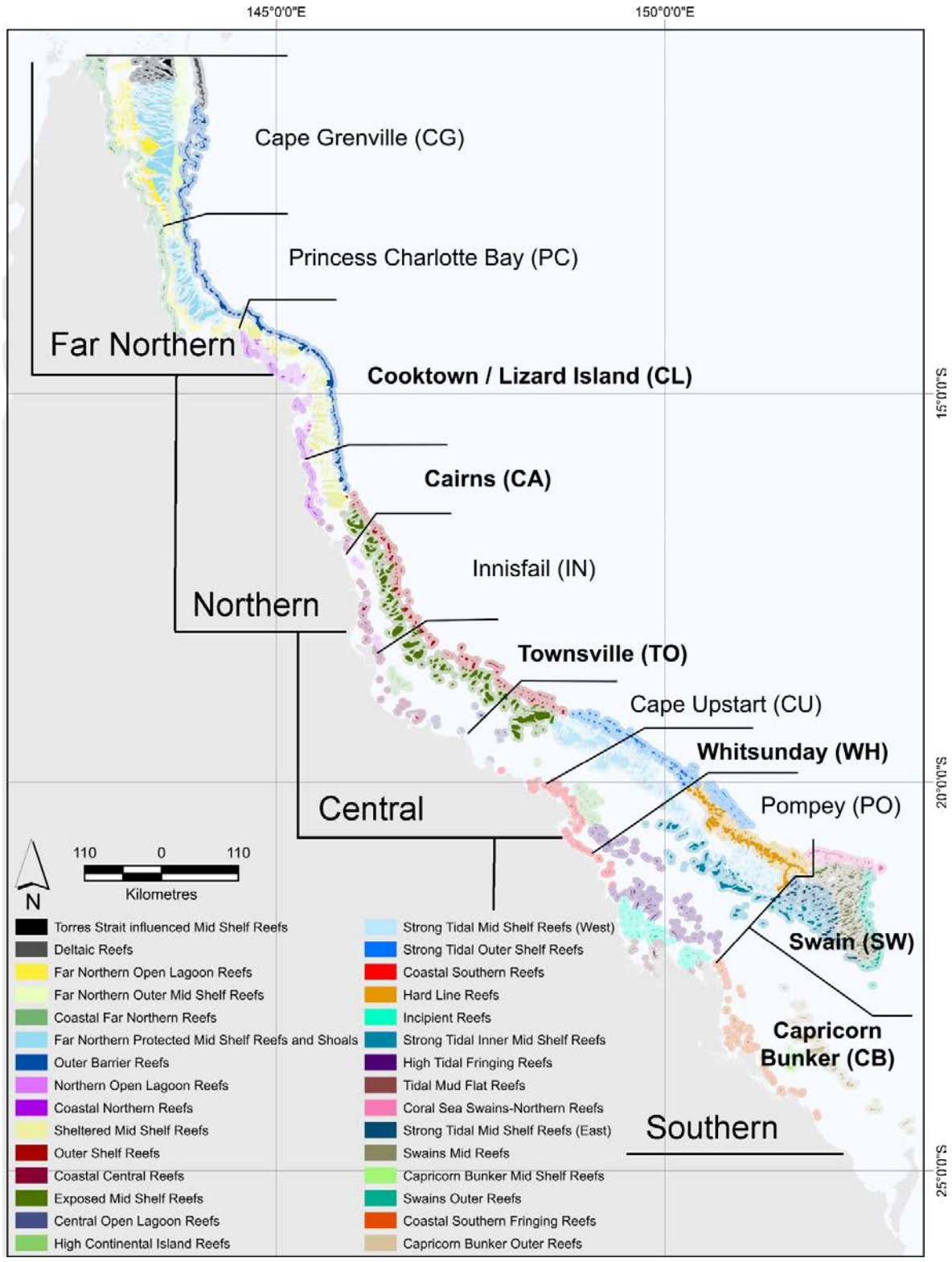

Figure 2.1 Marine Bioregions (colours) classifications defined by the Great Barrier Reef Marine Park Authority (GBRMPA), GBRMPA management areas (large latitudinal boundaries, e.g. Southern) and latitudinal sectors (smaller latitudinal boundaries, e.g. Swains (SW)) of the GBR surveyed as part of AIMS Long Term Monitoring Program.

2.3.1 Environmental and spatial data

The set of 30 environmental variables were collated nationally at a scale of 0.01° resolution (15,928 grid cells across GBR reef locations) by the Commonwealth of Australia's Environment Research Facility (CERF) Marine Biodiversity Hub (http://www.marinehub.org/). Environmental variables include long term average (1960-2006) and seasonal ranges of temperature and salinity as well as nitrate, oxygen, phosphate, and silicate concentrations. Averages (1997-2009) and seasonal variation are also provided for indices of ocean productivity (e.g., chlorophyll-a concentration); light attenuation (K490); benthic irradiance; and the strength and frequency of the combined wave–current bed shear stress. Bathymetric estimates (depth, aspect and slope) are single estimates derived from a 0.00025° grid developed by combining ship-track, swath and satellite data from 1963-2009. Sediment composition (mud, gravel, sand and carbonates) are interpolated from samples collected between 1960-2009. The variables provided were collated due to their importance as drivers of coral reef community structure (Pitcher et al. 2007) (see Table S 9.2 and data limitations for further details). In addition, spatial variables including the shortest distances to the coast and to the barrier reef were calculated for each grid cell of the GBR (using great-circle distance, i.e., the shortest distance between two points on the surface of the earth). Furthermore, we define the relative frequency of exposure to primary, secondary and tertiary flood plumes, representing turbid, sediment dominated plumes, chlorophyll dominated plumes, and the outer extent of plumes (as delineated by salinity less than 34ppt), respectively. These plume data were collated from remote sensing observations between 2007-2013 and are provided as a single estimate per grid cell. These data have been used as useful indicators of water quality including turbidity, productivity and plume extent (Devlin et al. 2012, Álvarez-Romero et al. 2013). Within this 0.01° resolution grid, reefs (as polygons) were categorised using the marine bioregion classification from the Great Barrier Marine Park Authority (GBRMPA) (Fig. S6), excluding any non-reef locations (e.g. cays, islands, mangroves).

2.3.2 Disturbance data

Spatial layers of disturbance exposure for each year during the study period (1985-2017) were compiled at a 0.01° resolution for coral bleaching, cyclones and *A.* cf. *solaris* outbreaks, representing the current state of knowledge regarding disturbance extent and severity on the GBR (Figure 2.2).

Heat stress exposure, which has been linked to coral bleaching, is presented as the annual maximum Degree Heating Weeks (DHW) (Figure 2.3). Satellite sea-surface temperature data from the National Oceanic and Atmospheric Administration (NOAA) CoralTemp dataset (https:/coralreefwatch.noaa.gov/satellite/coraltemp.php) at 0.05° (~5 km) resolution were used to calculate DHW values for 1985-2017. DHW values were determined using the standard Coral Reef Watch methodology (Liu et al. 2014, 2017). Data at 0.05° resolution were resampled using the nearest neighbour approach (assigning values from the nearest pixel) (Burrough 1986) to the nominal 0.01° grid. While there remains variation in bleaching response and subsequent mortality across reef sites of different composition and other environmental conditions, the use of the DHW algorithm in general has been successfully validated against empirical observation of bleaching events (Eakin et al. 2010, Heron et al. 2016, Hughes et al. 2017b). Additionally, this most recent version of the NOAA Coral Reef Watch DHW metric (Version 3, https://coralreefwatch.noaa.gov/satellite/bleaching5km/index.php) has been used to explain spatial patterns of mortality along the GBR following the 2016 bleaching event (Hughes et al. 2018a). Complementing these annual remote sensing data, extensive aerial surveys from the 1998, 2002 and 2016 bleaching events (Berkelmans et al. 2004, Hughes et al. 2018b) were interpolated (inverse distance weighted) to provide regional scale estimates of bleaching impact for these three extreme events. Categories used were as follows: 0 (<1% bleached), 1 (1–10% bleached), 2 (10–30% bleached), 3 (30–60% bleached), and 4 (>60%

bleached). Code and data to reproduce interpolation can be found at https://github.com/sammatthews990/GBRdata.

Cyclone exposure is presented as exposure to potentially damaging cyclonic seas (in hours per grid cell), where the highest one-third of waves were on average 4m or higher (4MW). The 4MW model developed by Puotinen et al. (2016) reconstructs the spatial distribution of cyclone winds of a range of speeds every hour for each of the 46 tropical cyclones that crossed the GBR during 1985-2016 at a spatial resolution of 0.04°. From this, the model calculates the duration of winds of various speeds for each cyclone, and together with estimates of fetch approximates the number of hours each location was potentially exposed to the *a priori* defined 'damaging' sea state. Testing with field data from seven cyclones on the GBR showed that the 4MW index outperformed previous methods for predicting a spatial zone beyond which severe cyclone damage does not occur even though damage within the zone is patchy (Puotinen et al. 2016). Data at 0.04° resolution were resampled using the nearest neighbour approach to the nominal 0.01° grid. Exposure to damaging seas from each of 46 cyclones were summed across the 0.01° to give a total yearly exposure to damaging waves. Data from cyclone Debbie, which crossed the GBR in 2017, is still being compiled and will be added to the dataset once the data becomes available.

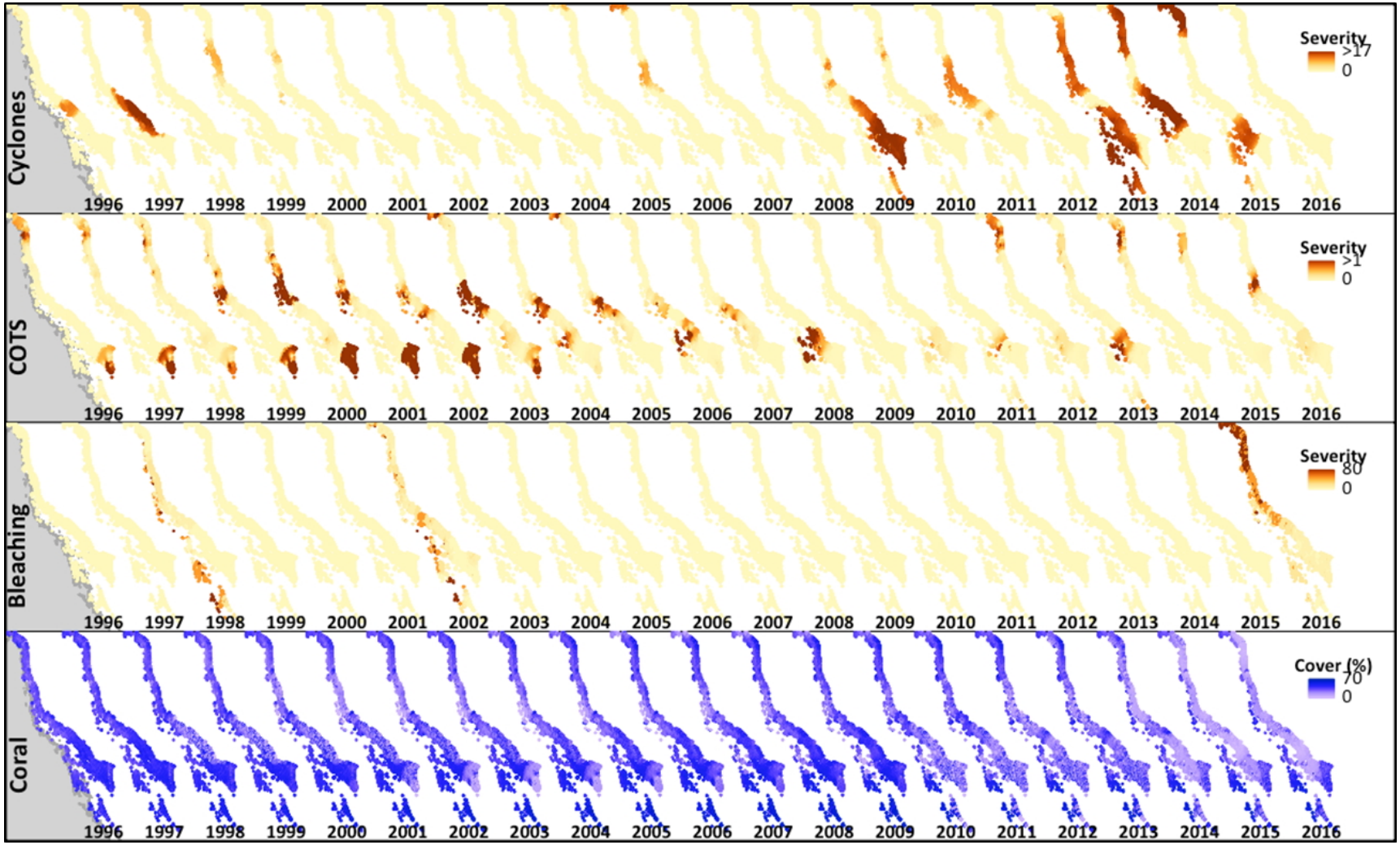

Figure 2.2 Maps of annual disturbance severity for tropical cyclones, outbreaks of the crown-of-thorns starfish (COTS) and coral bleaching, and predicted coral cover across the Great Barrier Reef. Shown are the number of hours of destructive waves generated by tropical cyclones (*row 1*); COTS mean density, with densities above 1 corresponding to active outbreaks (*row 2*), the percent coral cover bleached based on aerial surveys (*row 3*) and resulting predictions of coral cover generated by the model (row 4).

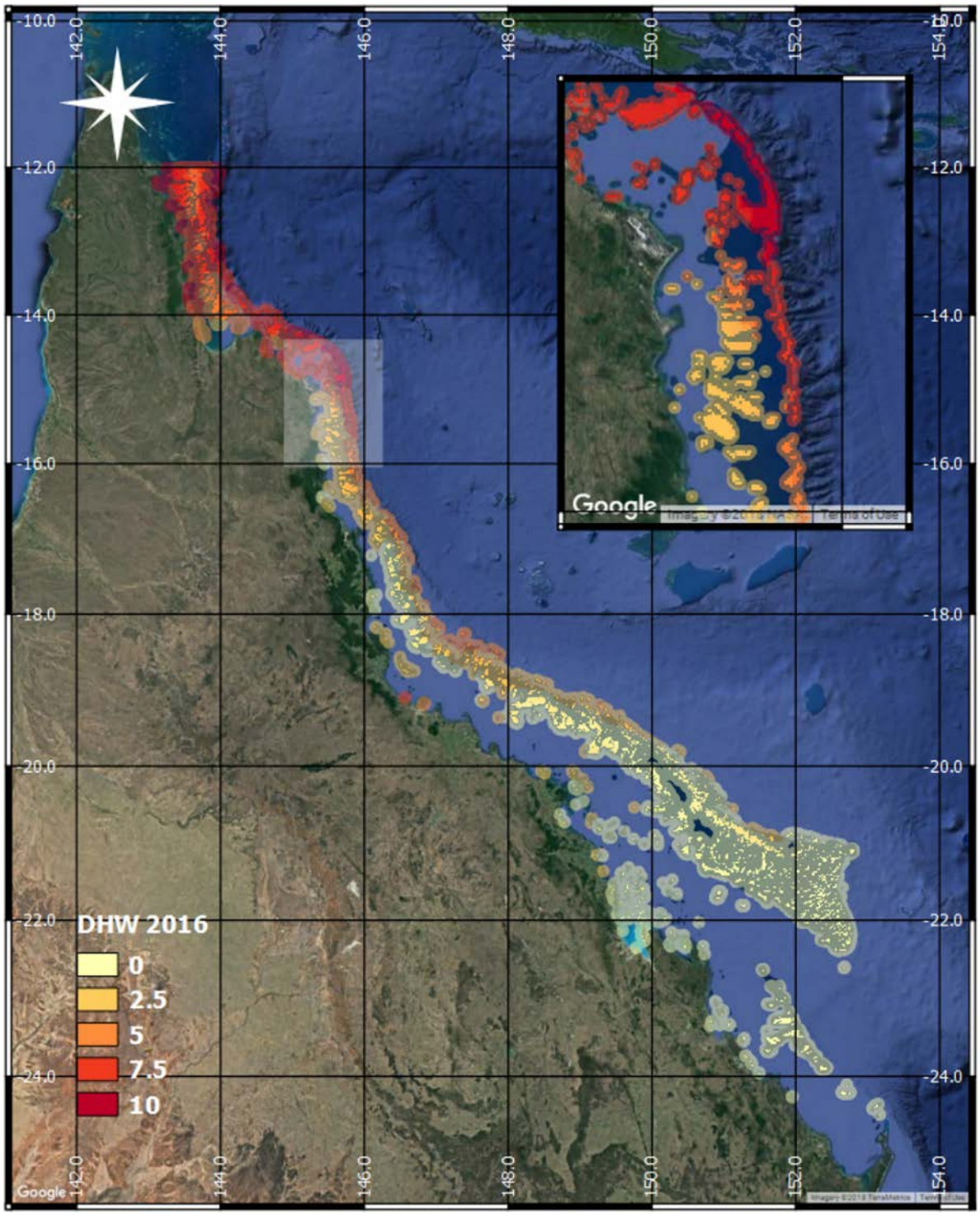

Figure 2.3 Annual maximum heat stress exposure measured as Degree Heating Weeks (DHW) for 2016, exemplifying the spatial resolution and extent of the dataset.

Annual estimates of mean *A.* cf. *solaris* densities were also generated by inverse distance weighting (maximum distance = 1°; minimum observations = 3) from the manta tow data

collected by the AIMS LTMP for every year between 1985 and 2017 (Miller and Müller 1999, Miller et al. 2009a). The LTMP surveys estimate *A.* cf. *solaris* densities for between 50-239 reefs annually (mean = 96 reefs). These empirical data consist of two-minute manta-tow observations (mean = 48 tows per reef), where observers are towed around the perimeter of each reef to search for *A.* cf. *solaris* individuals. The thresholds defining "incipient" and "active" outbreaks are defined as ≥ 0.22 and ≥ 1.0 individuals per two-minute tow respectively (Moran 1992, Sweatman et al. 2008, Pratchett et al. 2014). Interpolated values therefore represent the mean *A.* cf. *solaris* densities per manta tow as a guide to estimating coral loss. Code and data to reproduce interpolation can be found at https://github.com/sammatthews990/GBRdata.

2.4 Data Limitations

2.4.1 Environmental Data

There are a number of key limitations regarding the environmental data compiled in this dataset, namely the coarser resolution of original data (MARS, GEOMACS, CARS, MODIS, SeaWiFS) and the summarisation of temporal variability into static estimates rather than time series data. The variables were initially collected at the national level at a 0.01° resolution by the CERF Marine Biodiversity Hub (http://www.marinehub.org/) but are now maintained and made publicly available by Geoscience Australia. Full details of data collection for the compilation and further references can be found in Huang et al (2010). As environmental data in this compilation reflect a static estimate, temporal variation is addressed by the inclusion of the seasonal range variable, in addition to the mean over the entire times series where appropriate.

Bathymetry and Geomorphology (GA Variables)

National data was collated from surveys collected between 1963 and 2009, compiling approximately 1400 survey records combining ship-track, swath and satellite altimetry. The grid incorporates data from surveys acquired since 1963. Modern surveys that used GPS have

a positional accuracy of 5 - 30 m depending on several factors, while earlier surveys which used dead reckoning and Transit satellite fixes had positions accurate to 50-2000 m depending upon the water depth and strength of currents. These surveys overlap in an irregular distribution. As a number of approaches were used to process data and availability of data was variable, the resolution was reduced from ~0.0025° to 0.01° using inverse distance weighted interpolation to match the resolution of the satellite imagery used to infill areas without ship-track or swath data (Whiteway 2009, Huang et al. 2010). All temporal data were combined to produce a bathymetry layer with ~0.0025° resolution from which aspect and slope were derived. For all GA variables, spatial resolution was interpolated to 0.01° using inverse distance weighted interpolation.

Sediment Parameters (MARS Variables)

It is important to note that these variables were interpolated using the inverse distance squared weighted algorithm to achieve the 0.01° resolution from the National Marine Sediments Database (MARS - http://www.ga.gov.au/oracle/mars/), containing over 200,000 samples within the GBR region spanning 1960-2009. Importantly, the positional accuracy of the some of the older source data unknown but assumed to be within 5km. Users are urged to be cautious when drawing conclusions using these variables and to consult the MARS database or Huang et al. (2010) to assess regional uncertainty. For all MARS variables, spatial resolution was interpolated to 0.01° and all temporal data were combined to produce a single mean % sediment composition for each variable.

Geological and Oceanographic Model of Australia's Continental Shelf (GEOMACS Variables)

The GEOMACS model is a purely mathematical model with no direct field observations and does not include wave breaking or refraction. This model is thus not considered useful in depths

<10m (Huang et al. 2010) and users are urged to implement caution when using this variable in shallow water environments. For all GEOMACS variables, spatial resolution was interpolated to 0.01° using inverse distance weighting ((Huang et al. 2010). The temporal domain includes 11 years and therefore contains limited information on events with long return intervals at specific locations, e.g. tropical cyclones. GEOMACS variables are provided as two static estimates of mean and interquartile range estimated over the 11 years of data. The interquartile range is calculated as the difference between the Q25 and Q75 quartiles. The trimmed mean is the standard arithmetic mean calculated excluding the highest and lowest 25 percent of the GEOMACS model observations. The interquartile range and trimmed mean are not guided by ecological theory or observations but are generic statistical observations (Huang et al. 2010).

CSIRO Atlas of Regional Seas (CARS Variables)

The CARS2006 database was compiled from all historical subsurface ocean property measurements (Ridgway et al. 2002) derived primarily from research vessels and autonomous profiling buoys. Data was collected over approximately 50 years (~1960-2006) to create an estimate and seasonal range for temperature (deg. C), salinity (PSU), oxygen (ml/litre), nitrate (micromole/litre), silicate (micromole/litre), phosphate (micromole/litre). While some regions of the CARS database has insufficient data (e.g. southern NSW) this was not the case on the GBR (Huang et al. 2010). For all CARS variables, spatial resolution was interpolated from 0.5° to 0.01° using inverse distance weighting to match the resolution of this compilation. The temporal domain spans ~50 years and therefore these variables are to be used as long-term averages and indicators of seasonal variability and should not be used to analyse acute events.

Satellite Data (MODIS and SeaWiFS Variables)

The main consideration for the satellite-derived variables in this dataset is to appreciate that native resolution for the satellites (0.04°) was interpolated to 0.01°. Moreover, it is important to note that estimates for these variables are based on the monthly composites. Thus, seasonal ranges reflect the range of monthly means and mean estimates are the mean of monthly means. Whilst these estimates can be useful for understanding baseline conditions and variation, they should not be used where fine-scale temporal fluctuations are important, as these patterns are smoothed out in this dataset. Finally, these data were collected for the years 1999-2008 and 1997-2008 for MODIS and SeaWiFS respectively, and whilst representing a good estimate of the mean and variability of environmental conditions, they cannot be viewed as entirely representative of current or past conditions. These satellite derived variables are proxy indicators and thus their performance must be considered. Importantly, whilst general spatial patterns of Chlorphyll *a* and Kd490 (SeaWiFS) were captured, validation with *in situ* measurements in tropical north eastern Australia waters had poor accuracy if the inherent optical properties of the region were not considered (Qin et al. 2007). Moreover, SeaWiFS variables are not suitable for coastal waters, and therefore inferences must be cautious with regard to inshore GBR reefs (Devlin et al. 2012b). For all MODIS and SeaWiFS variables, spatial resolution was re-gridded from 0.04° to 0.01° by the authors of the original dataset (Huang et al. 2010) and temporal variation was captured as a seasonal range variable reflecting the range of monthly means across the times series. Where no data is available in a pixel due

to clouds or other interference, the previous 8-day average is carried forward in that pixel in this data set.

2.4.2 Disturbance Data

In contrast to the environmental data, disturbance data is provided for each year between 1985-2017 for COTS, Cyclones and DHW and for 1998, 2002, and 2016 for aerial bleaching surveys.

Crown-of-thorns starfish

A lack of empirical observations makes it difficult to validate predicted COTS abundances; further research into COTS population dynamics is under way to address this issue (Matthews et al., in prep). As there are significant spatial gaps in the AIMS LTMP data used to create spatial layers of COTS abundance, individual data points were interpolated to 0.01° resolution. In order for a value to be estimated, a minimum of 3 observations had to be found within a 1 degree radius for interpolation. This also means that there are many blank values as sampling for COTS is patchy and thus care must be taken to understand the temporal patterns before using these data. This makes the assumption that COTS will be present at all neighbouring reefs and does not take into account the array of environmental factors which make reefs suitable for COTS (Chapter 4) and thus should only be used as a starting point for regional scale models (Chapter 5-6) and not as a definitive estimate of COTS density at fine spatial scales.

Cyclones

The cyclone data presented were resampled from a native grid of 0.04° to the nominal 0.01° grid and represents every cyclone passing the GBR between 1985-2017. However, data were aggregated for each calendar year for consistency with other disturbance variables, so some years may contain the footprint of two or more cyclones (1986, 1990, 1993, 1996, 2000, 2009, 2011, 2015). Furthermore, these data represent exposure to *potentially* damaging waves, which

does not always result in coral mortality and does not take into account the potential shielding effect that may occur on the leeward side of reefs.

Bleaching Aerial Observations

Bleaching observations were interpolated from reef-level estimates of bleaching severity to the 0.01° grid for the 3 years for which surveys were provided (*sensu* Hughes et al. 2017). For 1998, 2002 and 2016 bleaching events 638, 631 and 1156 reefs were surveyed respectively across the length of the GBR, representing a substantial portion of the GBR (~3800 reefs) (Berkelmans et al .2004, Hughes et al. 2018).

Degree Heating Weeks (DHW)

Regarding heat stress, although the relationship between DHW and coral mortality has been established (Hughes et al. 2018a), fine scale patterns of bleaching are often patchy and thus hard to resolve from the relatively broad-scale satellite-derived products. Additionally, the DHW product used here assumes that an anomaly at the surface of the ocean can be accurately related to anomalies at greater depths. However, due to local hydrodynamics, this assumption is not always valid, limiting the ability to infer bleaching in deeper locations on the reef (Skirving et al. 2006). DHW products presented here were aggregated for the calendar year. These data were resampled from a native grid of 0.05° to the nominal 0.01° grid and thus should be considered carefully when investigating sub-reef processes.

It is important to stress that the DHW and Cyclone data have been resampled to the nominal 0.01° grid from more coarsely scaled products (DHW: 0.05°, Cyclones: 0.04°), while COTS data from manta tow surveys have been scaled up from fine-resolution reef observations onto the grid. This compromise of spatial scale is often a necessity in ecosystem modelling as the

spatial scales for biological data and environmental data vary greatly, but it is integral that users understand these compromises before using the product.

2.5 Conclusion

The disturbance history and abiotic context of the Great Barrier Reef is of central importance to any attempt to create accurate regional scale models. This initial data compilation acts as the platform upon which the modelling in the later chapters of this thesis will build upon, and importantly, as a template for regional scale modelling of the GBR in the broader research community. Whilst updates to the dataset will be required and improvements can be made to some variables, the compilation provides the first attempt to catalogue the abiotic environment and disturbance regimes for GBR reef locations with necessary resolution to facilitate regional-scale models.

3 Conservation intelligence: Integrated visualisation and reporting tools in support of adaptive pest management and ecological monitoring

3.1 Abstract

Adaptive management has become a dominant paradigm in natural resource management and conservation. Embedding adaptive management into conservation interventions is essential to continually improve management outcomes, but necessitates the ongoing assessment of the extent of the problem, the current knowledge, the associated uncertainty, available intervention strategies, monitoring techniques and evaluation of outcomes. These tasks are not trivial, and there is an ongoing need for improved data tools to facilitate and enhance the uptake of adaptive management approaches to conservation. Here we demonstrate the utility of adapting established Business Intelligence (BI) software to provide near real-time analytics and decision frameworks for effective adaptive management of conservation interventions and ecological monitoring. These tools, which we define as Conservation Intelligence (CI) tools, synthesise complex spatial and temporal data streams to provide managers with an interactive and easy-to-use interface to assess the extent of the problem, and to evaluate the progress of interventions. The utility of CI tools is demonstrated using crown-of-thorns starfish (COTS; *Acanthaster* cf. *solaris*) on Australia's Great Barrier Reef (GBR). On the GBR, outbreaks of these corallivorous pests have caused widespread decline in coral cover and are the target of one of the largest (geographically and economically) coral reef pest control programs in the world, coordinated and delivered by the Great Barrier Reef Marine Park Authority (GBRMPA). Our understanding of the extent and severity of these outbreaks and the

effectiveness of control actions to mitigate their impacts is integral to the adaptive management of this system. To this end a visualisation and reporting tool, *The COTS Dashboard*, was developed to visualise the severity and extent of outbreaks and evaluate the progress of the intervention against stated goals. The dashboard was developed in close partnership with GBRMPA, meaning the needs of the management agency were explicitly incorporated into each stage of the development process. The CI approach attempts to improve the effectiveness of the adaptive management cycle and to develop informative and flexible platforms embedded within the management agency, to assess and visualise progress towards conservation goals. Such initiatives provide managers with the interactive and user-friendly tools required to make adaptive data-driven decisions, ensuring the greatest strategic impact of conservation interventions.

3.2 Introduction

In a rapidly changing environment, there is increasing pressure to develop conservation interventions and governance arrangements that can respond to changes in the system and adapt to intensifying stressors (Folke et al. 2002, Olsson and Folke 2004, Hughes et al. 2005, Heller and Zavaleta 2008, Stein et al. 2013). The adaptive management framework (Holling 1978, Walters 1986)(Figure 3.1) has been adopted as an effective management tool to address such problems characterized by high levels of uncertainty (Gunderson and Holling 2002, Gregory et al. 2006, Anthony et al. 2015). However, there has been a lack of clarity regarding its appropriateness or feasibility due to the indiscriminate application of adaptive management where the burden of continual evaluation, stakeholder engagement and re-assessment has hindered or halted conservation outcomes (Gregory et al. 2006, Rist et al. 2013). One of the major issues with adaptive management lies in the reactive nature of the to acquire the necessary monitoring information, as funding cycles often lag behind conservation problems (Downs 1972, Hoey et al. 2016). Moreover, when funding is adequately provided and data are routinely collected, there are still lags in the retrieval of insight from this data due to the significant additional resources and ongoing commitment required to summarise, manage and

analyse data to inform decision making and to effectively communicate with stakeholders (Williams and Brown 2014). In large, spatially and temporally complex systems, managers are required to assess the extent of the problem, collate existing knowledge and identify areas of uncertainty while simultaneously tracking the progress of specific management targets. To successfully achieve conservation goals within the adaptive management framework, managers need to be equipped with tools to efficiently evaluate the effectiveness of interventions and to engage stakeholders at various stages of the process.

Newly developed Business Intelligence (BI) software provides an extremely flexible platform to synthesise and visualise complex ecological data from disparate data streams which can be used to effectively inform the adaptive management process. Interactive and informative data visualisations have been shown to be useful to this process by creating active engagement and knowledge generation amongst stakeholder groups (Keller and Tergan 2005, Evanko 2010) and by providing a vehicle for knowledge transfer between science, management and policy (McInerny et al. 2014). Despite the rapid increase in advanced data visualisation software, particularly in business and finance (Murugesan and Karthikeyan 2016, Ul-Ain et al. 2019),

there has been a slower up-take of interactive data visualisations within the fields of environmental management, science-for-policy, conservation and research.

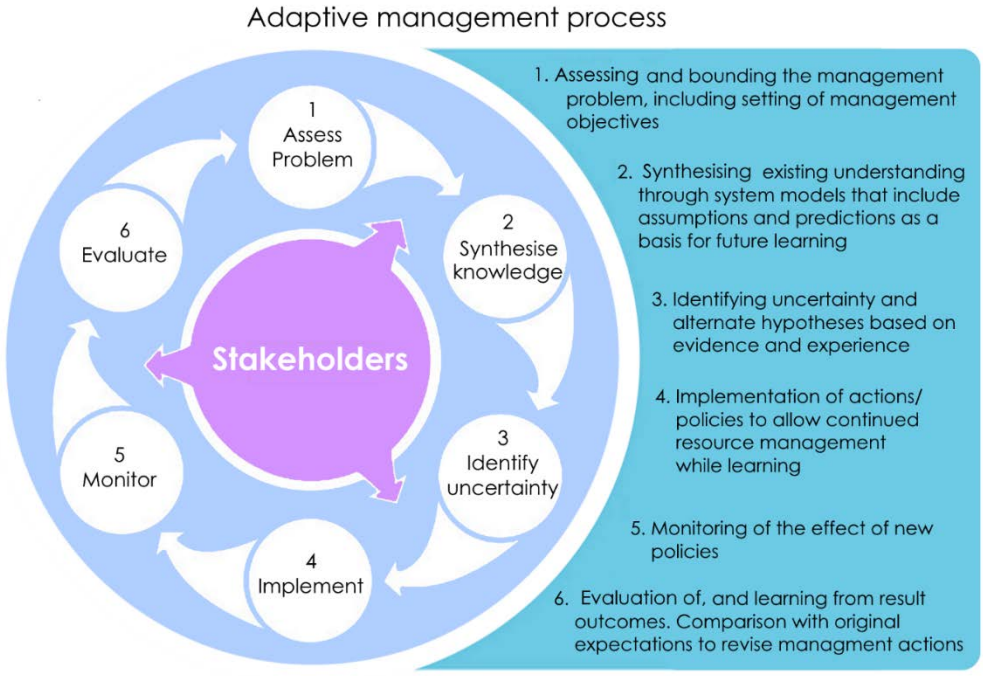

Figure 3.1 The adaptive management process (based on Walters (1986) and Holling (1978)) outlining the 6 major stages involved and the central role of stakeholder engagement in effective adaptive management; figure adapted from Rist et al. (2013).

In environmental management and conservation, task-specific decision support tools are commonly used in the adaptive decision-making process. For example, software such as Marxan (Ball et al. 2009), has been developed with the explicit purpose of designing marine reserves, and have been instrumental in the planning of many marine reserves globally, such as the rezoning if the Great Barrier Reef Marine Park (GBRMPA 2004, Ball et al. 2009). Such tools, despite being a powerful and necessary component of a strong conservation initiative, by design, are limited in their scope and can suffer from long term stability issues whilst often requiring software development or programming expertise (Pınarbaşı et al. 2017). Following low-frequency usage, many decision support tools are not maintained and become unavailable, causing issues for the agencies relying on them (Curtice et al. 2012, Pınarbaşı et al. 2017).

While decision support tools are essential for early stages of a conservation initiative, there is a need to improve the development and utilisation of tools for the evaluation of management

actions, monitoring, and the refinement of goals. There is a strong case for adapting freely available, easy to implement and maintain BI software to aide in these underrepresented stages of the adaptive management cycle. These software are already deeply entrenched in the business sphere and will only increase in functionality and technical support (Murugesan and Karthikeyan 2016), providing a stable platform from which to build visualisation and reporting tools that are adaptable to managers needs and evolution of the given management program. Adapting BI tools towards conservation goals (hereafter referred to as Conservation Intelligence (CI)), can provide user friendly, interactive platforms for managers and researchers to explore and communicate complex patterns in their data, evaluate and monitor management actions thus supporting adaptive decision making in conservation interventions.

The Great Barrier Reef Marine Park is widely considered as one of the leading examples of best-practice adaptive management in marine ecoystems, with extensive zoning regulation (Day 2002, GBRMPA 2004) , mature adaptive management frameworks (Hughes et al. 2007a, McCook et al. 2010b, Dobbs et al. 2011), protective federal legislation and extensive ecological monitoring (Hedge et al. 2017). However, despite best-practice adoption of management principles, the Great Barrier Reef (GBR) is still vulnerable to disturbances that threaten its resilience and ecosystem function. For example, coral cover on the GBR has declined by approximately 50% over the last 30 years (De'ath et al. 2012) and the increasing frequency and intensity of disturbances, exemplified by the recent mass bleaching events (Hughes et al. 2017b) and recurring outbreaks of the coral-eating crown-of-thorns starfish (COTS) (Pratchett et al. 2017a), suggests this pattern is likely to worsen (Pratchett et al. 2019). These declining trends in coral cover underpin an urgent need for effective and efficient management interventions to minimise coral loss on the GBR. Currently, on the GBR the largest conservation intervention aimed at directly minimising coral loss is the Crown-of-thorns Starfish Control Program (COTS Control Program). Outbreaks of COTS have been responsible for 40% of the decline in coral cover on the GBR over the last 30 years (De'ath et al. 2012) and culling adult or sub-adult individuals (using lethal injection (Rivera-Posada et al. 2014))

currently represents the most effective direct action to minimise coral loss from COTS outbreaks on the GBR (Westcott and Fletcher 2018).

Since 2012, the Australian Government has funded a COTS Control Program delivered through the GBRMPA, in order to reduce the impact of this marine pest. The COTS Control Program uses dedicated vessels and trained crews that perform targeted culling of COTS at strategically selected reefs of high ecological and economic value (Hoey et al. 2016). The methods utilised to achieve the management goals of the COTS Control Program have evolved over the last 5-6 years through an adaptive management process informed by collaboration between the GBRMPA, Commonwealth Scientific and Industrial Research Organisation (CSIRO), industry stakeholders, and leading COTS researchers, in order to deliver an increasingly integrated pest management approach to COTS Control (Fletcher and Westcott 2016, Westcott et al. 2016). The program collects extensive ecological data, which is essential for monitoring the status and condition of high value reefs prioritised for control, for developing and validating ecological models of COTS outbreaks and spread the GBR, and for tracking progress of the individual vessels and the intervention program as a whole. In the context of recent mass bleaching and mortality of many corals on the GBR (Hughes et al. 2017b, 2018a) there has been an increased commitment to preserving coral cover and recognition that COTS control is a feasible on-ground action to minimise coral loss and enhance the resilience of the GBR (GBRMPA 2017). Consequently, in 2018, the COTS Control Program underwent a three-fold increase in its operational fleet. The expansion of this program now enables the collection of unprecedented temporal and spatial resolution ecological data for the GBR. Within the context of COTS control, and also in the broader context of the monitoring needs of the GBR, there is an increasing need for data tools to efficiently synthesise, analyse and report on the state of the reef and the progress towards the stated goals of conservation interventions (GBRMPA and Queensland Government 2015, Hedge et al. 2017).

Herein we present The COTS Dashboard as an example of a CI tool for data visualisation, reporting and assessment of the COTS Control Program on the GBR. The COTS Dashboard is designed to address four key components of the Control Program; 1) Provide an ecological

overview of the system; 2) Assess progress of the Program on designated priority reefs; 3) Assess the performance of the vessel providers contracted to deliver the program and 4) Provide a user-friendly interface for creating customisable summaries to share with program stakeholders and research partners. We highlight how developing these CI tools provide managers with the interactive and user-friendly information required to make adaptive, data-driven decisions and foster efficient stakeholder engagement, ensuring the greatest strategic impact of conservation interventions. More broadly, we demonstrate the usefulness of these tools as a flexible and stable complement to bespoke decision support systems for pest management, ecological monitoring and conservation initiatives in general.

3.3 Methods

3.3.1 Data collection

For the COTS Control Program, each of the control vessels collects three types of observational data. Manta Tow observations, in which an observer is towed around the perimeter of a reef (Miller et al. 2009a) are conducted to generate a broad-scale understanding of the coral cover and COTS abundances at a given reef. In the context of integrated pest management, these surveys are also used to determine whether culling action is required at the reef and site (Fletcher et al. in prep). Culling action is triggered by either the observation of an adult COTS or COTS scars. Once culling action has begun at a reef, the number of COTS culled is recorded in four size classes; 0-15 cm, 15-25cm, 25-40 cm; >40 cm alongside the number of diver minutes undertaken during cull activity. Each reef is split into equal sized (8-10Ha) culling sites, which are "opened" following the observation of adult COTS or presence of COTS scars. All sites across the reef with these signs of COTS activity are culled repeatedly, and then "closed" once culling activity has reduced catch-per-unit-effort (COTS culled per dive minute) below ecologically sustainable thresholds (CPUE = 0.04 COTS per minute) (Fletcher et al. in prep., Babcock et al. 2014). Subsequent Manta Tow observation are conducted every ~3-6 months to determine whether the population is controlled, and sites are re-opened if COTS or scars are observed again. Reef Health Impact Surveys (RHIS) (Beeden et al. 2014)

(observations within a 5m radius of reef location) are also conducted at sites where pest management action is undertaken in order to monitor coral health.. The joint Field Management Program (FMP) and the Queensland Parks and Wildlife Service (QPWS) also collect extensive Manta Tow and RHIS surveillance data which is integral to informing prioritisation of control efforts. In total, the COTS Dashboard synthesises data collected from >30,000 RHIS surveys, >52,000 Manta Tows and > 10,000 culling dives across >900 reefs, averaging >10,000 surveys per annum.

3.3.2 Data extraction, transformation and loading (ETL)

One of the most important features of CI tools, such as the COTS Dashboard, is the capability for flexible data extraction, transformation and loading (ETL). The COTS Dashboard was built in Microsoft Power BI, which (like other BI software) includes powerful data connectivity and preparation capabilities (using PowerQuery) that allow users to integrate hundreds of different data sources and reshape and transform them to suit their needs, without requiring coding skills. For the COTS Control Program, data is predominantly entered via android apps in the field and stored in the GBRMPA's Eye on the Reef Database (Beeden et al. 2014). However, some legacy datasets and spatial data are stored and maintained internally as spreadsheets which are integrated with other sources within the COTS Dashboard back-end. Importantly, data cleaning, and merging is easily handled within the Power BI platform, allowing these different data sources to be quality-checked before being analysed and reported on.

3.3.3 Data relationships

In order for CI tools to provide interactive filtering and aggregating of data, the relationships between the data tables must be described, creating a relational database upon which more complex analytics can be carried out. While BI software will auto-generate relationships between data tables containing similar identifiers (i.e ID columns and dates) they are best described explicitly. In the COTS Dashboard, observational data (Manta Tow, Culling and RHIS) are linked to a table holding spatial data for every one of the 3863 reefs in the GBRMP, to allow all forms of observational data to be filtered simultaneously by spatial identifiers (i.e

Reef Name, Marine Park Zone, Management Sector) (Figure 3.2). Similarly, the data for each observation is linked to a separate table containing generic temporal data, allowing all observational data to be filtered and analysed over a common time scale (Figure 3.2).

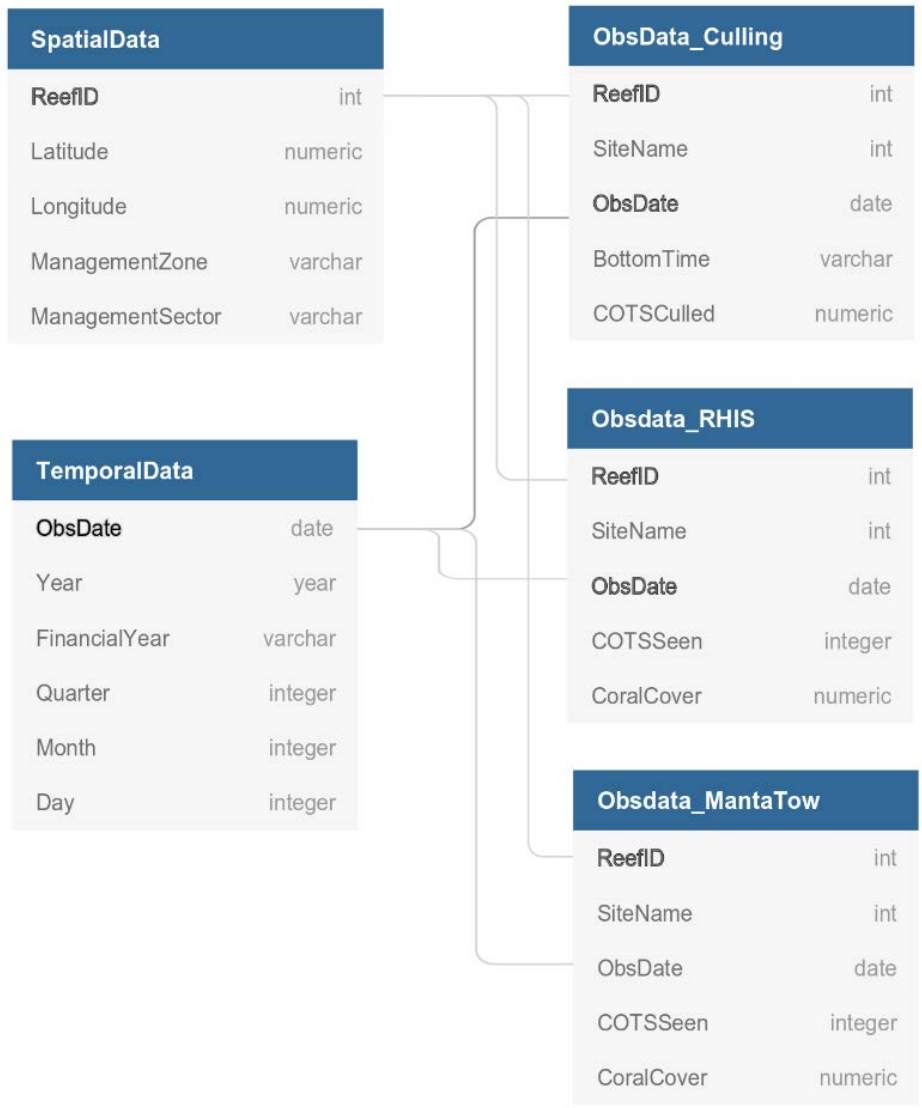

Figure 3.2 Simplified representation of the relational database structure constructed within the COTS Dashboard. Variables highlighted in bold represent the primary keys used to link tables together.

3.3.4 Design process

Addressing the needs of managers to make adaptive decisions is fundamental to the successful development, integration and utilization of data tools in conservation. As these needs often change or shift focus, throughout the implementation of a conservation initiative, it is

imperative to have consistent direct feedback from end users. The COTS Dashboard was thus developed on-site at the GBRMPA ensuring the explicit needs of Marine Park managers were incorporated throughout the design process, and allowing end users to gain familiarity with the platform's capabilities. Importantly, explicit targets and thresholds of the COTS Control Program are central to the COTS Dashboard, with visualisations and summaries being designed to highlight progress towards these goals.

3.4 Results

The major applications of CI tools in general, and the COTS Dashboard in particular, involve the ability of these tools to address specific stages in the adaptive management cycle (Figure 3.1). Here we present four key applications of the COTS Dashboard:

1) Provide conservation managers at the GBRMPA with the most up-to-date information on the current (and historical) extent of COTS outbreaks in a spatially and temporally explicit manner (Stage 1), whilst incorporating contemporary theoretical knowledge of the system (Stage 2) and estimating uncertainty (Stage 3).
2) Provide a platform to track the implementation of COTS management interventions by vessel providers (Stage 4);
3) Monitor the progress of these implemented management actions in achieving the ecological goals of the Control Program (Stage 5) and evaluate whether the management action had the desired outcome (Stage 6);
4) Produce engaging visualisations alongside easily obtained and flexible data summaries as tools for stakeholder engagement throughout the adaptive management process.

3.4.1 Synthesise current understanding: Assessing COTS outbreak status

One of the key requirements for managers of the COTS Control Program is efficiently synthesise data coming from multiple monitoring and control vessels to generate up-to-date estimates of the distribution of COTS across the GBR. To serve this purpose, the first page of the COTS Dashboard (Figure 3.3) portrays the "Outbreak Status" of each reef with available

data, alongside a summary table, providing further insight into the data and uncertainty of the attributed "status". Internally, the Dashboard is compiling several datasets to produce reef level estimates. This overview of the current state of the system can also be filtered interactively by the user, by adjusting a time "slicer" to inspect historical patterns, or by selecting zoning regulation, management sector or outbreak status itself to inspect spatial patterns in COTS outbreaks. Providing the historical and current context of the severity and extent of COTS outbreaks gives spatial and temporal bounds to the ecological problem to help set objectives (Stage 1). The incorporation of ecological thresholds to determine outbreak status reflects the ability to build in assumptions of the current understanding of COTS outbreaks (Stage 2). Finally, uncertainty in estimates are included in summary tables (as standard error) or revealed when hovering over a reef location (Stage 3). Temporal uncertainty can also be investigated by moving the time slicer.

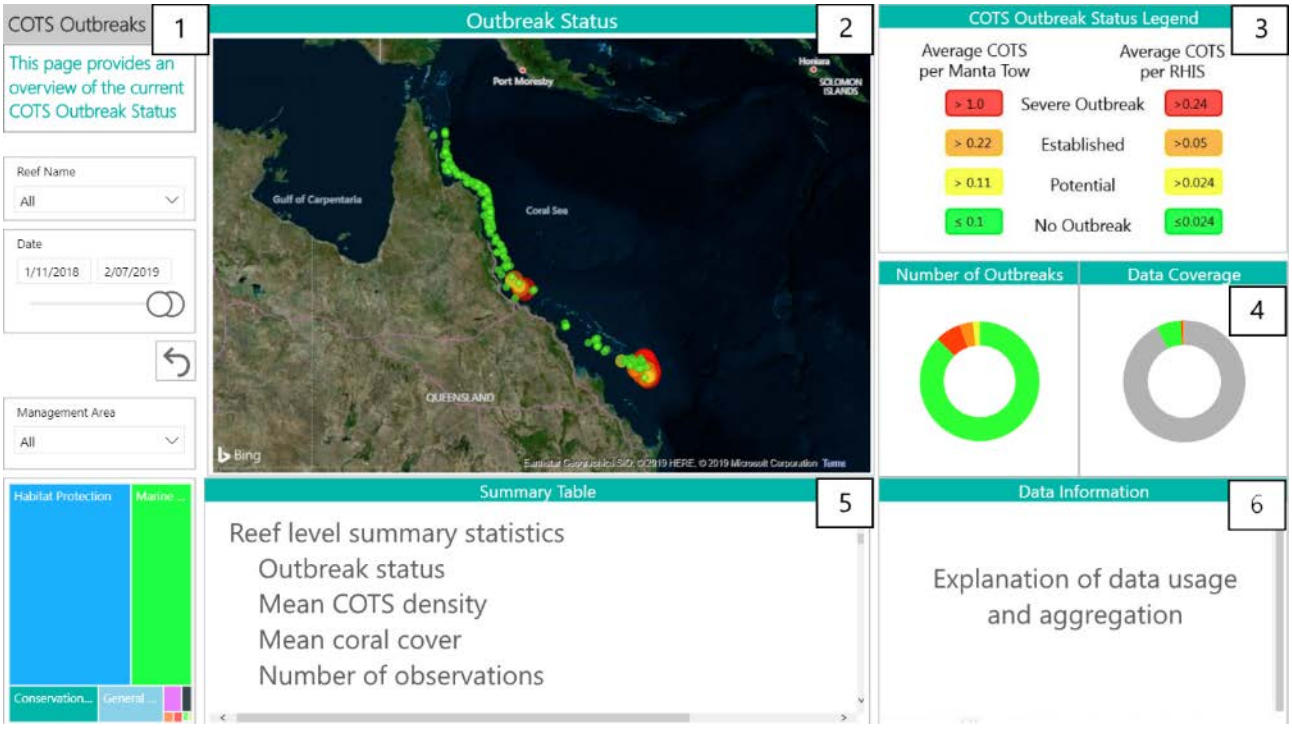

Figure 3.3 Outbreaks status page of the COTS Dashboard. The page contains 1) An input panel of "slicers" for filtering data by reef name, date, region and zoning regulation; 2) map of current outbreak status (relative to Date slicer); 3) Legend for 2) highlighting established thresholds for COTS outbreak status; 4) Filterable donut charts the proportion of reefs within each outbreaks category and the proportion of reefs across the Marine Park for

which we have current data; 5) Summary table of latest estimates of COTS densities, coral cover and number of surveys; 6) Information box explaining the temporal aggregation of data and usage of survey methodologies.

3.4.2 Implement management actions: Integrated pest management process

The ability to monitor how management actions are being implemented in the field is integral to managing the COTS Control Program. Specifically, the COTS control program requires vessels to undertake initial surveillance of a reef to determine where culling activities should begin, as part of an integrated pest management approach (Fletcher et al. in prep, Fletcher and Westcott 2016, Westcott et al. 2016). Culling "sites" are then opened and culled on subsequent voyages until COTS densities are restricted below established ecological thresholds. Reef wide surveillance is also conducted every 2-3 months to monitor the COTS densities and coral cover. The COTS Dashboard provides a page dedicated to tracking the implementation of this pest management process (Figure 3.4), allowing users to select a reef of interest, view initial (or any subsequent) surveillance data and the ensuing culling operations. These types of visualisations provides users with an interactive platform for tracking the implementation of management actions, ensuring the integrated pest management process was followed in the deployment of culling resources (Stage 4).

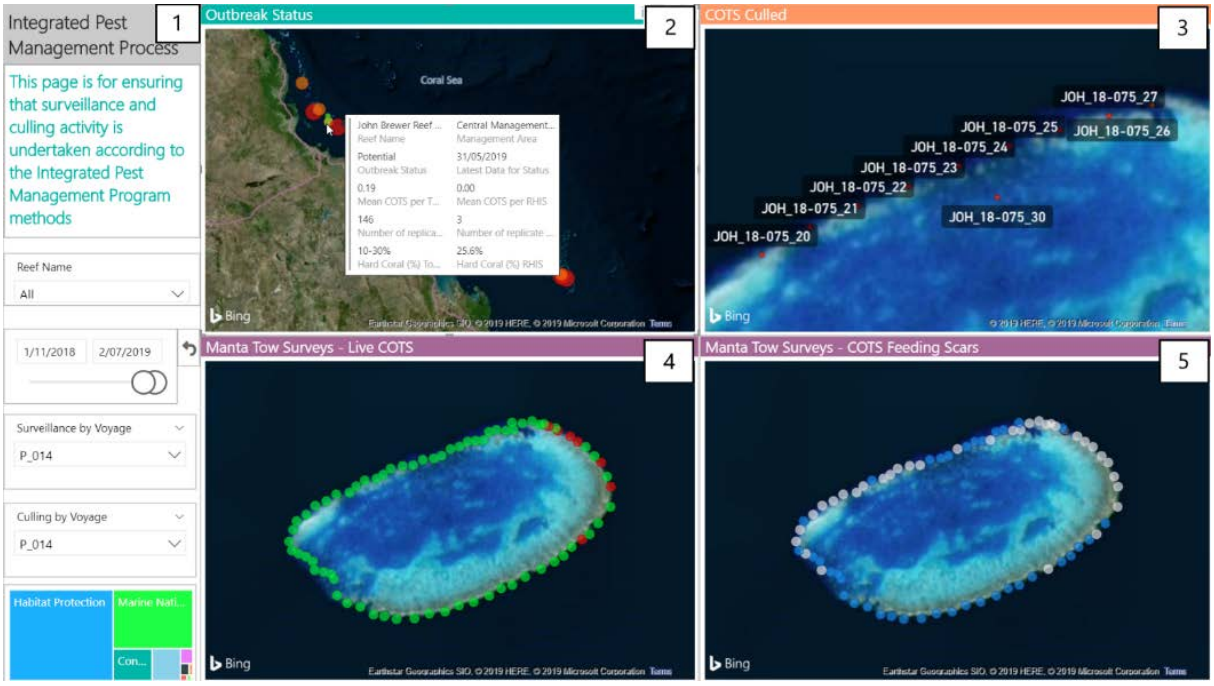

Figure 3.4 Integrated pest management page of the COTS Dashboard. The page contains 1) An input panel of "slicers" for filtering data by reef name, date, voyage and zoning regulation; 2) map of current outbreak status

(relative to Date slicer) with "tooltip" of summary data; 3) Map of culling activity at sites for the selected reef/voyage 4) Map indicating the presence of COTS (green = absent; red = present) for the selected surveillance voyage; 5) Map indicating the presence of COTS feeding scars (blue = absent; white = present (1-10); grey = common (>10) for the selected surveillance voyage.

3.4.3 Monitor the effect of actions: Progress towards management goals

The COTS control program aims to reduce COTS densities to specific thresholds on reefs that are prioritised by culling. Visualisations within the COTS Dashboard allow managers to quickly assess progress towards achieving this goal at a site, reef or regional level. Specifically, the COTS Dashboard has a page dedicated to synthesising culling data (Figure 3.5). By selecting a reef from a list or from the map, managers can view the catch per unit effort (CPUE) of COTS over time and monitor the progress toward reaching the ecological threshold (Stage 5). Furthermore, each culling site within the reef can then be selected in order to compare site and reef level trends and investigate the spatial variability in catch-per-unit-effort. Importantly, time series data can be aggregated at the Year, Quarter, Month or Voyage level allowing users to increase or decrease the temporal resolution of their analysis. Additionally, as reefs are closed for culling, this page provides the opportunity to evaluate the outcomes against the initial expectations (Stage 6). For example, the assessing the number of hours and repeated culling

trips required to achieve the goals allows management to refine the expectations and modify the approach for various outbreak densities of COTS.

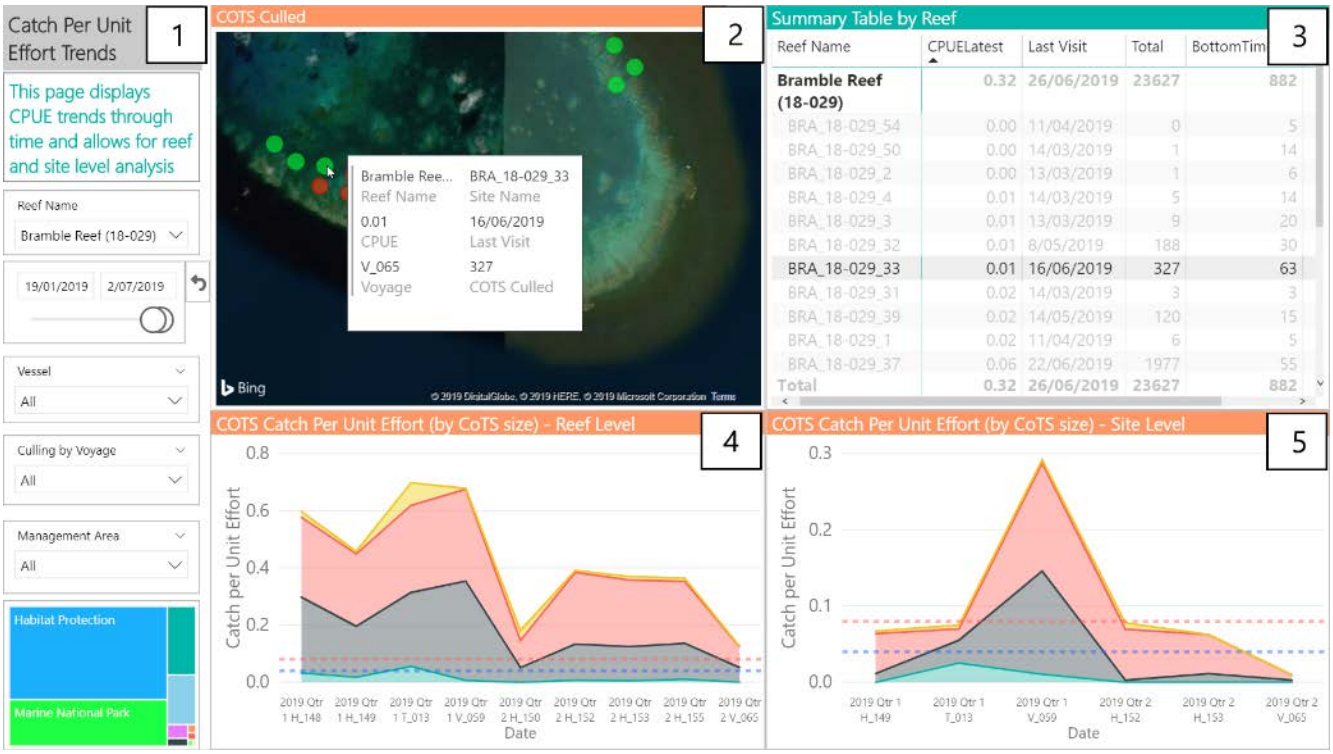

Figure 3.5 Catch per unit effort (CPUE) trends page of the COTS Dashboard. The page contains 1) An input panel of "slicers" for filtering data by reef name, date, voyage and zoning regulation; 2) Map of most recent culling activity at sites for the selected reef/voyage with "tooltip" of summary data (green = below cull threshold 0.04; red = above cull threshold; 3) Summary table providing reef and site level summaries 4); CPUE trends (colours represent different size classes of COTS: green=0-15cm; grey=15-25cm; red=25-40cm; yellow=40+cm) at the selected reef level, highlighting progress towards ecologically sustainable thresholds 5) CPUE trends at the site level (selected by 2) or 3)) to compare the progress of individual sites within a reef to the broader reef level trends.

3.4.4 Stakeholder engagement: Data summaries and visualisations

As the COTS Dashboard are simply visualisations built upon a relational database, it is a simple process to create ad-hoc summaries or visualisations for special purposes. For example, the GBRMPA has many research partners involved with the development of the control program and in COTS research more broadly and thus receives many requests for data. These requests vary greatly in their temporal and spatial scope as well as the level of aggregation required (i.e. site/reef/region or voyage/month/year). Having a tool such as the COTS Dashboard allows these requests to be addressed promptly while reducing the potential for error associated with manually creating summaries in a spreadsheet. Additionally, the diverse array of visualisation

options (Microsoft Power BI 2019) provides a useful tool for creating summary graphics for a variety of stakeholder audiences, or for communicating Program outcomes to higher level managers and policy makers.

3.5 Discussion

The COTS Dashboard provides a user-friendly interface, to understand and assess the severity and extent of COTS outbreaks, track the implementation of management actions and monitor progress towards stated goals. Importantly, such CI tools are completely customisable and require limited technical proficiency, making them an ideal, but as yet under-utilised platforms for adaptive management and ecological monitoring. COTS outbreaks evolve in complex temporal and spatial patterns (Vanhatalo et al. 2017), occurring in patchy aggregations at the sub-reef level (Ormond and Campbell 1974) and displaying cryptic behaviour (Pratchett et al. 2014) making the control and monitoring of their outbreaks an intrinsically difficult task. Managers of the Great Barrier Reef have the difficult task of tracking and responding to emerging or established outbreaks over time, across a Marine Park that spans 344,400 km^2 and encompasses 3864 reefs. Ensuring that these complex spatial and temporal patterns of outbreaks across the GBR are understood by managers, policy makers, contractors and researchers, is integral to implementing an effective COTS Control Program. As the Control Program relies on many stakeholders spanning socio-political boundaries it is also vitally important to develop efficient platforms for stakeholder engagement. The COTS Dashboard, and CI tools more broadly, can facilitate knowledge exchange of complicated ecological problems among a diverse array of stakeholders. While access to the Dashboard is currently unavailable outside of the GBRMPA, advances are being made to allow wider access as part of the broader Reef 2050 Integrated Monitoring and Reporting Program (RIMReP) (Dobbs et al. 2011, Hedge et al. 2017).

Specifically, the Dashboard helps reef managers address the stages of the adaptive management cycle (to varying degrees) whilst fostering stakeholder engagement from a single platform. From the main page, managers can stay up-to date with the incoming data from the control

program allowing them to assess the current (and historical) extent of COTS outbreaks (Stage 1). The dashboard also synthesises the available contemporary knowledge (Stage 2) of COTS outbreaks by comparing COTS densities and catch per unit effort trends to important modelled thresholds for outbreak densities (De'ath 2003, Babcock et al. 2014). Additionally, it provides a platform to identify uncertainty (Stage 3) within the control program by providing information on the number, standard error of estimates and spatial coverage of surveys used to estimate COTS abundances and coral cover. It also provides a platform to track the implementation of COTS management interventions by vessel providers (Stage 4); The dashboard collates the data necessary to monitor and evaluate the effectiveness of the program (Stages 5 and 6) by tracking the progress towards goals (reducing COTS to sustainable levels, reducing coral cover loss). Additionally, while not the explicit purpose of the Dashboard, it can be used as means to identify errors within the databases, to identify outliers or spatially mismatched observations. Most importantly however, is the flexibility of the platform, whereby any changes to management goals (e.g. altered thresholds or changing prioritisation of reefs) can be amended without requiring a software developer or extensive IT experience.

On the GBR, there has been a concerted effort in recent times to develop reporting and integrated monitoring frameworks to inform the adaptive management of the GBRMP (Dobbs et al. 2011, Hedge et al. 2017). In particular, the GBRMPA is pursuing the development of interactive reporting tools (e.g. Power BI) because they were identified by the majority of survey participants (> 75%) as the ideal type of platform to deliver the Reef 2050 Integrated Monitoring and Reporting Program (GBRMPA and Queensland Government 2018). CI tools such as the COTS Dashboard provide an important template and proof-of-concept for the successful delivery of an integrated monitoring and reporting program at the GBR scale. More broadly, developing CI tools is an important step forward for the global conservation movement. Over the last few decades there has been a vast increase in the number of monitoring programs and conservation initiatives, and whilst effective design is key to success (Legg and Nagy 2006, Guerra et al. 2019), the efficient management, analysis and communication of insights from the data are integral steps in generating knowledge from an

integrated monitoring framework (GBRMPA and Queensland Government 2018). As conservation initiatives mature, CI tools will play an increasingly important role in disseminating insight from programs and aiding in their adaptive management.

Interactive data visualisations are becoming recognised as increasingly important to engage and educate relevant audiences, particularly in the context of science for policy and stakeholder engagement (McInerny et al. 2014). By providing an interactive platform to interrogate complex spatial and temporal data, CI tools aim to improve data literacy and knowledge transfer of the system for researchers, managers, stakeholders and policy-makers alike. However, understanding the realised impact of decision support (and CI) systems and stakeholder engagement on conservation outcomes remains somewhat elusive. Although there is some disagreement regarding the effectiveness of stakeholder engagement (Reed 2008, Young et al. 2013), increased levels can have important flow on effects, increasing trust and the perceived likelihood of a successful outcome (Young et al. 2013). Additionally, in the business world, effective BI systems are generally accepted to increase productivity, improve decision-making performance, and enrich knowledge (Trieu 2017). The increased adoption of these BI tools in the conservation sphere could reap similar benefits. Despite the uncertainty regarding the concrete measurable outcomes of such tools, the development of effective visualisations, such as the COTS Dashboard, is regarded as one of the most pressing concerns for scientists and science policy (McInerny et al. 2014). Importantly, with respect to the COTS Control Program, the GBRMPA are obliged to engage stakeholders, particularly in sharing data collected through the program, and thus the development of CI tools is a necessary step in maturing a large publicly funded conservation program.

The COTS Dashboard was developed alongside the major end user (GBRMPA), thereby avoiding some of the major challenges associated with bespoke decision support tools (Pınarbaşı et al. 2017). More specifically, extensive understanding of the data needs of the end users from the outset increased engagement and greatly reduced development costs (McIntosh et al. 2011). We also intentionally used established software, which is thoroughly documented and supported, which importantly, can be created and modified independent of expert

developers. However, the use of commercial software does have some drawbacks, especially the inability to edit source code and uncertainty about long-tern access and availability to the product. More broadly, CI tools are applicable to any ecosystem and can be applied to any conservation initiative or monitoring project where interactive visualisations/summaries may be useful to understand complex patterns. There are multiple platforms upon which they can be built (Microsoft Power BI, Tableau, QlikView), and while these platforms are generally built to serve the business analytics industry, their capabilities go far beyond these applications. Importantly, the low cost (free in some cases) and relatively lower level of technical ability required to design such a tool makes CI tools readily available to small scale conservation initiatives, NGO's, government departments or researchers without requiring a significant software development budget. Moreover, CI tools can also be adapted towards a research orientated focus, particularly for sharing complex model outputs among collaborators and lay-people, allowing uncertainty and parameter sensitivity to be viewed interactively. CI tools incorporate interactive visualisations, simple GIS capabilities, extensive options for data integration, easy to share reports and web apps (paid subscriptions), making them ideal platforms for pest management, marine spatial planning and ecological monitoring initiatives.

3.6 Conclusion

The construction of a specific and dedicated CI interface (the COTS Dashboard) has provided a number of benefits and efficiency gains for the COTS Control Program. The COTS Dashboard has greatly reduced time spent on the repetitive, non-reproducible and error-prone production of graphs and summary statistics within the Program. CI tools are extremely flexible and can be easily expanded to include new streams of modelled or empirical data as new research and management actions are implemented. More broadly, CI tools enable the effective implementation of adaptive management, particularly by increasing the user's ability to assess the state of the problem, identify uncertainty, and monitor and evaluate the progress of conservation interventions, whilst providing a platform for stakeholder engagement. This

project highlights that currently available and accessible software can effectively address some of the foremost challenges to adaptive management in data-rich and complex systems.

4 Connectivity and water quality explain distribution and abundance of Crown-of-thorns Starfish across the Great Barrier Reef

4.1 Abstract

Outbreaks of the coral eating crown-of-thorns starfish (COTS; *Acanthaster* cf. *solaris*) occur in cyclical waves along the Great Barrier Reef (GBR), contributing significantly to the decline in hard coral cover over the past 30 years. One main difficulty faced by scientists and managers alike, is understanding the relative importance of contributing factors to COTS outbreaks such as increased nutrients and water quality, larval connectivity, fishing pressure, and abiotic conditions. We analysed COTS abundances from the most recent outbreak (2010-2018) using both boosted regression trees and generalized additive models to identify key predictors of COTS outbreaks. We used this approach to predict the suitability of each reef on the GBR for COTS outbreaks at three different levels: (1) reefs with COTS present intermittently (Presence); (2) reefs with COTS widespread and present in most samples and (Prevalence) (3) reefs experiencing outbreak levels of COTS (Outbreak). We also compared the utility of two auto-covariates accounting for spatial autocorrelation amongst observations, built using weighted inverse distance and weighted larval connectivity to reefs supporting COTS populations, respectively. Boosted regression trees and generalized additive mixed models were combined in an ensemble model to reduce the effect of model uncertainty on predictions of COTS presence, prevalence and outbreaks. Our results indicate that larval connectivity potential is the best predictor of COTS outbreaks (relative importance = 22.7%) while flood plume exposure (Presence=18.5%, Prevalence = 15.6%), chlorophyll concentration (Presence=15.3%, Prevalence = 20.5%) and temperature variables (Presence=23.1%, Prevalence = 7.5%) were among the most important predictors of COTS presence and

pervasiveness on a reef. Interestingly, whether the reef was open or closed to fishing had no significant effect on COTS presence or outbreaks. We identified major hotspots of COTS activity primarily on the mid shelf central GBR and on the southern Swains reefs. This study provides the first empirical comparison of the major hypotheses of COTS outbreaks and the first validated predictions of COTS outbreak potential at the GBR scale incorporating connectivity, nutrients, biophysical and spatial variables, providing a useful aid to management of this pest species on the GBR.

4.2 Introduction

Outbreaks of the corallivorous crown-of-thorns starfish (*Acanthaster* cf. *solaris*) occur on the Great Barrier Reef (GBR) approximately every 15 years (Kenchington 1977, Reichelt et al. 1990b, James and Scandol 1992, Lane 1996, Seymour and Bradbury 1999) and have been responsible for up to 40% of the loss of hard coral cover on the GBR over the last 30 years (De'ath et al. 2012). Long term data suggest that outbreaks originate in the northern GBR within Cairns-Lizard Island region, known as the "initiation zone" (Wooldridge and Brodie 2015, Vanhatalo et al. 2017). These are known as primary outbreaks, and are characterised by the build-up of COTS densities through local recruitment during repeated successful spawning seasons (Endean 1974, Johnson et al. 1992, Stump 1996, Pratchett et al. 2014). Inevitably, larger population sizes of adult COTS in the "initiation zone" overcome Allee thresholds (Rogers et al. 2017), enhancing fertilisation and increasing propagule pressure, seeding downstream secondary outbreaks (Endean 1974, Pratchett et al. 2014). As the outbreak progresses, aided by the prevailing south-easterly flow of the East Australian Current, these secondary outbreaks spread southward down the GBR in "waves" (Kenchington 1977, Pratchett et al. 2014). Although the spatial patterns in the progression of an outbreak are somewhat consistent, predicting which reefs will be affected by an outbreak remains elusive.

While oceanographic patterns of larval dispersal (Scandol and James 1992, Hock et al. 2014, Uthicke et al. 2015a), and the anthropogenic erosion of natural population regulation ('terrestrial run-off hypothesis' (Birkeland 1982) and 'predator removal hypothesis'(Endean

1969)) are commonly used to explain the initiation of primary COTS outbreaks, the majority of reefs affected by COTS on the GBR are subject to the waves of secondary outbreaks. Understanding the spatial patterns of these secondary outbreaks and the role of their environmental drivers remains a key research and management knowledge gap (Pratchett et al. 2017a). While recent research has used estimated larval connectivity networks to explain which reefs might be sources or sinks of COTS larvae across the GBR (Hock et al. 2014), it did not account for other important environmental drivers of COTS outbreaks (e.g. chlorophyll-a (Fabricius et al. 2010)), nor did it allow for the distinction between primary and secondary outbreaks.

The density of COTS can vary greatly both within and among reefs over short time scales (Birkeland and Lucas 1990, Pratchett et al. 2014). This spatial and temporal variability of COTS populations indicates that there may be important differences between the drivers of COTS presence on a reef, and the drivers of COTS outbreaks (>0.22 individuals per manta tow (De'ath 2003, Sweatman et al. 2008)). Additionally, at a reef level, COTS are often found in patchy aggregations presumably linked to coral prey availability (Chesher 1969, Pratchett et al. 2017a) and to enhance fertilisation potential in spawning aggregations (Babcock et al. 1994, Rogers et al. 2017). Such patchiness suggests that the prevalence (herein referred to as the proportion of tows in which COTS are observed) of a COTS outbreak on a reef may again be linked to subtly different environmental and ecological drivers than COTS presence or outbreaks.

Although several major hypothesis have been put forward to explain COTS population fluctuations, they generally fall into three major categories 1) Larval-nutrient supply hypotheses 2) Predatory release hypotheses and 3) Larval connectivity hypotheses, all underpinned by the immense fecundity and fast maturation of COTS individuals, making them naturally predisposed to large population fluctuations (Vine 1973, Antonelli and Kazarinoff 1984, Uthicke et al. 2009, Babcock et al. 2016b, Mellin et al. 2016b). Enhanced nutrient levels since European settlement have been shown across multiple laboratory studies to have positive effects on COTS larval survival (Fabricius et al. 2010, Uthicke et al. 2015b, Wolfe et al. 2015,

2017, Pratchett et al. 2017b), while others have highlighted the confluence between elevated nutrient supply major and COTS outbreaks (Fabricius et al. 2010, Wooldridge and Brodie 2015, Brodie et al. 2017). Some support for predatory release hypotheses has been provided by the reduced likelihood and intensity of COTS outbreaks on reefs with "no-take" zones closed to fishing (Sweatman 2008, Vanhatalo et al. 2017). These studies indicate that increased fishing pressure on large predatory fish, diminishes their ability to regulate COTS populations, thereby increasing of the risk of outbreaks, but these studies did not account for any other influential covariates other than latitudinal and cross-shelf location. While some progress has been made to identify potential predators of adult and juvenile COTS (Cowan et al. 2017a), it is still unclear how much changes to fish populations may affect the initiation and spread of COTS outbreaks. Finally, the recently developed hydrodynamic models for the GBR have been used to identify important source and sink reefs across the GBR network (Hock et al. 2014) and to help design decision frameworks to increase the effectiveness of COTS control on the GBR (Hock et al. 2016). These predictions are based entirely upon the potential larval connectivity estimates and assume all reefs have the same suitability for populations of COTS. An important extension of these models, is to explicitly incorporate known (and potential) drivers of COTS outbreaks and spatial patterns in COTS observation data. Most importantly these predictions should be validated against the available observation data to understand the associated uncertainty.

Although COTS dynamics on the GBR are clearly influenced by a combination of factors, there has yet to be an attempt to empirically assess the importance of each of these competing hypotheses in a single study. Babcock et al. (2016a) provided the first qualitative assessment of competing hypotheses, focusing on the role of nutrients and predation in mediating COTS population dynamics. While being a useful theoretical framework to understand COTS population dynamics, their model was not validated against empirical data and did not explicitly include larval connectivity. During the current outbreak cycle (2010-2019) there has been a vast expansion in the COTS control program, providing unprecedented monitoring data on COTS populations across a large extent of the GBR (Figure 4.1). This increased spatial and

temporal resolution of observation data and the availability of GBR-wide estimates of environmental variables and connectivity estimates provides a unique opportunity to compare competing hypotheses in a spatially explicit manner. Importantly, they also provide an opportunity to investigate how these variables drive the presence, outbreaks and prevalence of COTS populations.

Species distribution modelling (SDM) is a powerful tool for predicting the spatial distribution of a species and identifying the relative importance of their environmental drivers across landscapes (Guisan and Thuiller 2005, Leathwick 2009, Franklin 2010, Robinson et al. 2011). The nature of many ecological relationships are often non-linear and recently machine learning approaches such as boosted regression trees (BRT) have been increasingly used to predict species ranges and identify important predictor variables (De'ath 2007, Elith et al. 2008, Sutcliffe et al. 2014). These approaches are often conducted in an ensemble model with generalized additive models (GAM) that can also account for non-linear trends by applying a smoother, providing useful flexibility for fitting ecologically realistic relationships in SDM (Leathwick 2009). Importantly, for species with dynamic ranges such as COTS it is important to include covariates pertaining to important biotic interactions and dispersal pathways in an SDM approach (Elith et al. 2010, Mellin et al. 2016b). SDM provides empirical and validated predictions of reefs most likely to experience COTS outbreaks while also modelling the relative importance of each of the competing hypotheses and their relationship to COTS.

More specifically, this study will:

(1) Identify key environmental, spatial and hydrodynamic drivers that may explain spatial patterns of COTS presence, outbreaks and prevalence across the extent of the GBR:
(2) Construct an ensemble model to compare the relative influence and relationships between candidate predictors and COTS populations;
(3) Compare the utility of contemporary COTS larval connectivity estimates over simple distance estimates of connectivity for accounting for spatial

autocorrelation and

(4) Derive predictive maps of COTS presence, outbreaks and prevalence to help identify potentially important reefs for COTS control operations.

4.3 Methods

4.3.1 Crown-of-thorns Starfish Observation Data

Two independent sets of COTS observation data were gathered: 1) manta tow data from the Australian Institute of Marine Science Long Term Monitoring Program (AIMS LTMP), and 2) combined manta tow observations collected by the Great Barrier Reef Marine Park Authority's (GBRMPA) COTS control program and the Joint Field Management Program's COTS Response Program (collected by the Queensland Parks and Wildlife Services) (Figure 4.1). The data used here represent the most recent, spatially and temporally extensive observational data for COTS. The AIMS dataset spans from 1983 to 2019, whereas the other datasets were collected between 2012-2019 and thus the temporal extent of this study has been limited to the most recent outbreaks of COTS (2012-2019). Due to the substantial culling activity and tourism in the Northern management area, sampling intensity is greatest in these regions, however substantial data has been collected in the Central and Southern GBR (Figure 4.1). Manta tow data from the FMP and the Control program was collated to calibrate the models, and the AIMS LTMP data was used to independently validate model predictions. However, using data from only the most recent outbreak (since 2009/09) may reduce the model's performance in predicting the historical spatial distribution as this can vary between outbreak cycles (Figure 2.2). This is addressed partially by validating model predictions against the 30 year AIMS LTMP dataset to test performance against historical trends. At least two complete manta-tows during the 2012-2019 period were required for a reef to be included in the analysis. In total 335 reefs were included for model fitting with observations for 113 reefs used for model validation.

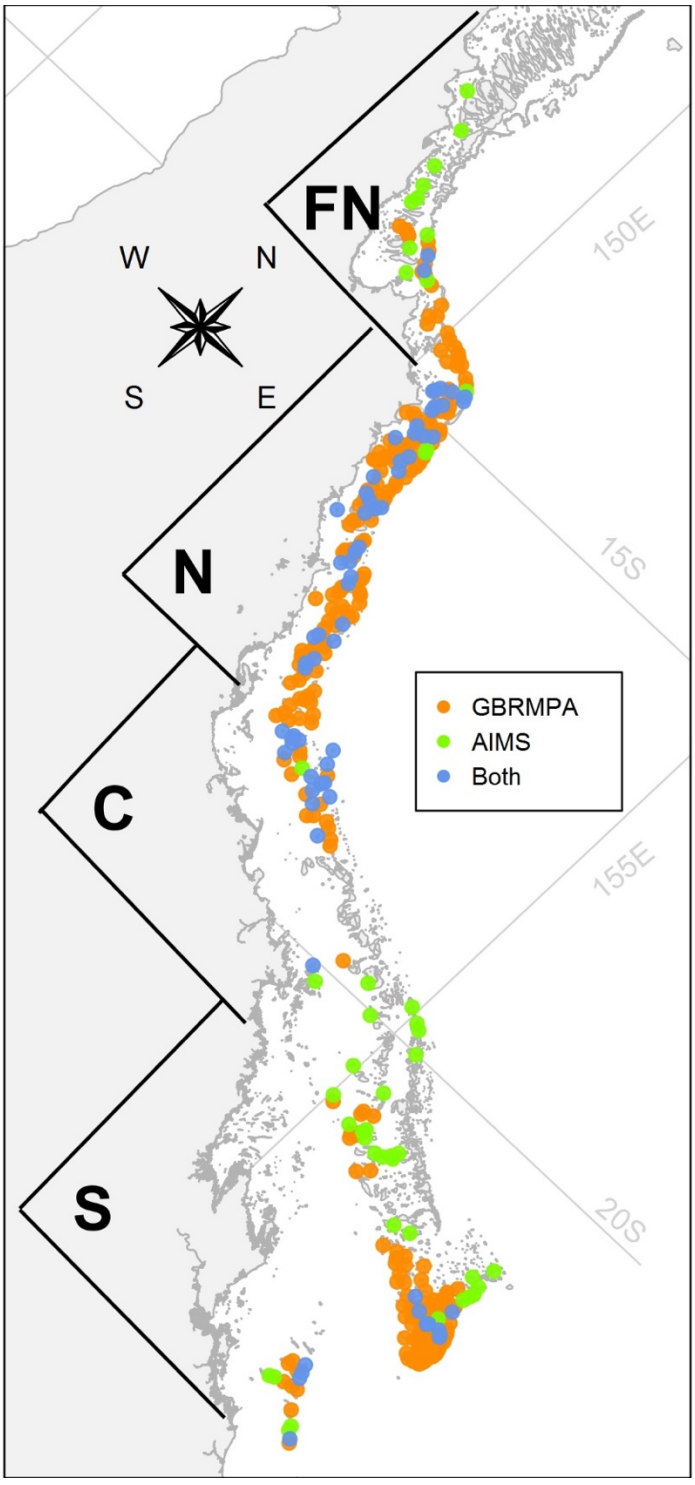

Figure 4.1 Reefs with available COTS observation data collected between 2012-2018, surveyed by either GBRMPA (Orange: COTS Control Program and the joint Field Management/Queensland Parks and Wildlife Services COTS Response Program) or Australian Institute of Marine Science Long Term Monitoring Program (Green) across the management areas of the GBRMP (FN=Far Northern, N= Northern, C=Central, S=Southern. Reefs surveyed by both institutions are shown in blue.

4.3.2 Response Variables

Survey data were collated at the reef level and presence of COTS was defined as any observation of COTS during manta tow observations of that reef (0-1; Present/Absent). Outbreaks at a reef were defined as per AIMS guidelines (De'ath 2003, Sweatman et al. 2008) for manta tow data (>0.22 COTS/manta tow) (0-1; whether or not COTS had reached outbreak levels) and fitted using a binomial distribution. Prevalence of COTS at a reef was defined in this study as the proportion of tows where COTS were observed during a set of manta tow observations (a survey: observer towed around the perimeter of a reef (Miller et al. 2009a)). As reefs are towed multiple times throughout the study period, the maximum recorded prevalence was used as the response variable to reflect the upper limits of COTS prevalence per reef (Figure S 9.3). Using the maximum prevalence is biased towards high density observations of COTS. This is by design as the aim is to identify predictors of reefs that are susceptible to populations of COTS that are distributed widely across the focal reef. This approach does make the model susceptible to sampling intensity which was partially accounted for by using only reefs that had been surveyed at least twice over the study period. The prevalence proportion was logit transformed prior to model fitting using a gaussian distribution (Warton and Hui 2011). For COTS prevalence a two-step modelling approach was used to accommodate for the zero-inflated nature of the proportion data (Cragg 2006, Potts and Elith 2006). Also called the hurdle model, this approach uses the results from the COTS presence model to define suitable reefs and then models the prevalence on suitable reefs only (e.g. (Mellin et al. 2012). The

dataset was thus restricted to contain only reefs that have been observed to host COTS at least once before modelling the major predictors of COTS prevalence.

4.3.3 Candidate Predictor Variables

All predictor variables used within this analysis were originally compiled on a 0.01° (~ 1km) grid across the GBR (Matthews et al. 2019) over various time scales (Table 4.1). These data were then averaged at the reef level to match the spatial scale of the observation data.

4.3.3.1 Water Quality Variables

Estimates of water quality were included as potential predictors for COTS distribution patterns due to the suggested effect of water quality on COTS larval development, survival and outbreaks. Water quality was considered in the study using satellite derived estimates of flood plume exposure (Devlin et al. 2012a, Matthews et al. 2019) and annual model estimates of mean and standard deviation of chlorophyll-a concentration (CSIRO 2019). The average frequency of exposure to primary (turbid, sediment dominated plumes) and secondary (chlorophyll dominated plumes) flood plumes was calculated across the GBR as the proportion of weeks within the Australian wet season where exposure to the plume type occurred between 2000-2014 (Devlin et al. 2012a). Daily estimates of chlorophyll concentrations were obtained from the eReefs 4km biogeochemical model (CSIRO 2019) 2013-2018 (all available data), and then annual mean and standard deviation were computed for each reef.

4.3.3.2 Disturbance Variables

GBR-wide estimates of mean annual exposure to potentially damaging waves generated by tropical cyclones and Degree Heating weeks (as an index of bleaching risk) (1986-2012) alongside exposure to the 1998 and 2002 bleaching events (Matthews et al. 2019). COTS typically prefer fast growing *Acropora spp.* corals (Pratchett et al. 2014), which despite being particularly susceptible to acute disturbances (e.g Hughes et al. 2018), recruit abundantly and often recover rapidly following disturbances (Linares et al. 2011, Osborne et al. 2011, Sato et al. 2018). COTS populations are thus presumably mediated by the disturbance history of a reef,

which are broadly captured by our indices of historical exposure to cyclonic waves, thermal stress and bleaching.

4.3.3.3 Environmental Variables

Static estimates of environmental variables, originally collated from the Commonwealth of Australia's Environment Research Facility (CERF) Marine Biodiversity Hub (Huang et al. 2013), were obtained from Matthews et al. (2019) over varying time scales (Table 4.1). These environmental variables include: annual mean estimates of nitrate, oxygen, phosphate, silicate, temperature and salinity, bathymetry, percentage cover of sediment components, multiple indices of the strength and frequency of the combined wave–current bed shear stress and spatial variables of minimum distances to the coast and the ocean at the edge of the GBR lagoon (Table 4.1). These variables have been successfully used to predict benthic community composition (Mellin et al. 2019a), fish assemblages (Mellin et al. 2010a) and other inter-reef species richness and abundance on the GBR (Sutcliffe et al. 2014). Moreover the dataset includes estimates of a number of variables shown to be important in affecting different life history stages of COTS such as salinity, oxygen and water temperature (Table 4.1).

4.3.3.4 Coral Variables

Estimated maximum coral cover and benthic community were obtained from Mellin et al. (2019a). Benthic communities were identified using multivariate regression trees (De'ath 2002), modelling the relationship between spatial and environmental covariates (Matthews et al. 2019) and the relative cover of benthic groups and coral taxa. Clusters of reefs were then defined by the multivariate regression tree corresponding to distinct taxonomic assemblages, characterized by its indicator taxa. The six benthic communities identified were: (i) outer reef – soft coral dominated; (ii) outer reef – digitate coral dominated; (iii) outer reef – tabulate coral dominated; (iv) mid shelf reef – mixed assemblage; (v) inner shelf reef – *Porites* dominated; (vi) Inner shelf reef – macroalgae dominated (Figure S 9.1).

Maximum coral cover, an index of the amount of substrate available or reef carrying capacity, was estimated from a 22-year time series at the 46 long term monitoring sites on the GBR based

on a Gompertz model of coral growth (MacNeil et al. 2019, Mellin et al. 2019a). This model assumes that in the absence of disturbance, coral cover increases from its initial value ($\boldsymbol{HC_{ini}}$, in 1996 in this case) to its asymptote ($\boldsymbol{HC_{max}}$, determined by the reef carrying capacity or amount of available substrate).

4.3.3.5 Spatial Variables

Outbreaks of COTS are spatially patchy yet are more common within the mid-shelf reefs on the GBR and with some evidence suggesting higher outbreak probabilities at reefs open to fishing (Sweatman 2008, Vanhatalo et al. 2017). To account for latitudinal and longitudinal patterns we included the cross-shelf location (inner, middle, outer) and four latitudinal sectors (Southern, Central, Central-Northern, Far Northern). Additionally, the effect of zoning on COTS populations was included as a categorical indicating whether a reef was open or closed for fishing (i.e. no-take area).

4.3.3.6 Larval Connectivity Variables

On the GBR the development of advanced hydrodynamic and larval connectivity models (Condie et al. 2012, CSIRO 2019) has facilitated the development of larval connectivity networks for COTS (Hock et al. 2014). These networks are constructed from 4 years of hydrodynamic modelled data and estimate the potential connectivity between all reefs on the GBR (2009-2013). Potential connectivity is a simplification of real-world processes which essentially represents maximal physically possible advective transport among reefs as implied by the model and expressed as a proportion of simulated larvae reaching destination reefs (Hock et al. 2014). As our COTS observational dataset spans 9 years, and our goal is to highlight the most important factors promoting COTS outbreaks, we used an averaged connectivity network that identifies the most consistent between-reef larval connections across years. From this network we computed the weighted in-strength for every reef, defined at the reef level as the sum of the potential connectivity from every other reef on the GBR. A reef with high in-strength will be characterised by high potential connectivity from many source

reefs, thus potentially representing an important sink for COTS larvae. The in-strength *s* of a reef *i* is defined as

$$s_i = \sum_j w_{ij}$$

- where w_{ij} is the potential connectivity from reef i to reef j (Barrat et al. 2004).

4.3.4 Spatial Autocorrelation

Outbreaks of COTS on individual reefs are not independent of one another, as an outbreak at one reef will likely seed an outbreak at a neighbouring reef if there is sufficient larval supply

via ocean currents (hereafter connectivity). Connectivity between reefs and spatial correlation of environmental drivers means there will be spatial autocorrelation within our response variables. To account for this autocorrelation we adopted the autologistic model (Dormann et al. 2007) where a distance-weighted term (the auto-covariate) is added to the predictor set, to represent the influence of neighbouring observations.

The auto-covariate **A** at any site i is calculated as:

$$A_i = \sum_{j \in k_i} v_{ij} y_j$$

where y_j is the response value of **y** at site j among site i's set of k_i neighbours; and v_{ij} is the weight given to site j's influence over site i (Augustin et al. 1996, Gumpertz et al. 1997). We calculated two competing auto-covariates: (i) a distance auto-covariate, whereby observations at site j were weighted by their inverse geographical distance to site i, and (ii) a connectivity auto-covariate, whereby observations were weighted by the estimated larval connectivity from site j to site i. Including the spatial auto-covariates allows the model to account for autocorrelation, but also allows the comparison of estimates of larval connectivity for COTS (Hock et al. 2014) to estimates based solely on distance. Additionally the connectivity auto-covariate models the larval connectivity to reefs that have experienced outbreaks, compared to

the in-strength variable which measures how well connected the focal reefs is to all others within the network, regardless of the outbreak status of those reefs.

Table 4.1 Predictor variable definitions, units, code used in SDM analyses: Env = envrionmental; WQ = water quality; Spat = Spatial; Cor = coral; Dist = disturbance; Conn = connectivity; = AutoCov = auto-covariate. References are provided for the source of the data and how these variables relate to COTS populations. *Indicates references that relate to the effect of the variable on COTS' coral prey and not COTS directly.

Type	Code	Description	Units	Years	Source	COTS Reference*
Env	O2_SR	Seasonal range oxygen	$mL.L^{-1}$	1960-2006	(Huang et al. 2010, Matthews et al. 2019)	(Lamare et al. 2014, Hardy et al. 2014)
Env	NO3_AV	Average nitrate	µM	1960-2006		(Birkeland 1982)
Env	S_AV	Average salinity	PSU	1960-2006		(Lucas 1973, Allen et al. 2017, Caballes et al. 2017b)
Env	S_SR	Seasonal range salinity	PSU	1960-2006		
Env	BATHY	Seafloor depth	m	1963-2009		(Johnson 1992)
Env	STRESS	Percentage of time for which the bed shear stress was > 0.4 Pa (Wave exposure proxy)	%	2010		(Moran 1986)
Env	SST_MIN	Minimum sea surface temperature	ºC	1999-2008		(Kamya et al. 2014, Lamare et al. 2014)
Env	MUD	percentage of a seabed sediment sample that is smaller than 63 µm in diameter	%	1960-2009		(Wolanski et al. 2003)*
WQ	WQ_1	Primary (representing turbid , sediment dominated plume) flood plume frequency (weeks occurred/total weeks) during wet season (max = 26).	Relative frequency (0-1)	2000-2014	(Devlin et al. 2012a, Matthews et al. 2019)	(Fabricius et al. 2010, Wolfe et al. 2015, Wooldridge and Brodie 2015, Pratchett et al. 2017b, Brodie et al. 2017)
WQ	WQ_2	Secondary chlorophyll dominated plume	Relative frequency (0-1)	2000-2014		
WQ	WQ_3	Further extent of plume, as delineated by salinity less than 34ppt	Relative frequency (0-1)	2000-2014		
WQ	CHL_A	Wet season mean	$mg\ m^{-3}$	2012-2018	(CSIRO 2019)	

	V	chlorophyll				
WQ	CHL_SD	Wet season standard deviation chlorophyll	mg m^{-3}	2012-2018	(CSIRO 2019)	
Spat	SHELF	Cross shelf location (Inner, Middle, Outer)	Factor (3 Levels)	-	(AIMS 2019)	(Moran 1986)
Spat	SECTOR	Marine Park Latitudinal Sector (Southern, Central, Northern, Far Northern)	Factor (4 Levels)	-	(GBRMPA 2014a)	(Moran 1986, Fabricius et al. 2010)
Spat	ZONE	Open or closed to fishing	Factor (2 Levels)	-	(GBRMPA 2014b)	(Sweatman 2008, Vanhatalo et al. 2017)
Cor	BENT_CL	Benthic coral community type	Factor (6 Levels)	Estimated 2018	(Mellin et al. 2019a)	(Lucas 1984, Pratchett 2007, Caballes et al. 2017a)
Cor	HC_MAX	Predicted maximum hard coral cover	0-100%	Estimated 2018		(Lucas 1984, Caballes et al. 2017a)
Dist	DHW_EXP	Mean exposure to degree heating weeks 1985-2012	Num	1985-2012	(Heron et al. 2016, Matthews et al. 2019)	(Kamya et al. 2014, Lamare et al. 2014)
Dist	CYC_EXP	Mean exposure to cyclonic waves (>4m) 1985-2012	Num	1985-2012	(Puotinen et al. 2016, Matthews et al. 2019)	(Osborne et al. 2011, Sato et al. 2018)*
Dist	BL_EXP	Mean exposure to 1998 and 2002 bleaching events	1-5	1998,2002	(Berkelmans et al. 2004, Matthews et al. 2019)	(Hughes et al. 2018a)*
Conn	IN_STR	Weighted sum of strength of incoming connections	Num	2009-2013	(Hock et al. 2017)	(Hock et al. 2014, 2017, Wooldridge and Brodie 2015)
Conn	LAR_RET	Estimated proportion of larval retention	%	2009-2013		
Auto Cov	AC_DIST	Auto-covariate weighted by distance to reefs with COTS present	Num	-	(Dormann et al. 2007)	
Auto Cov	AC_CONN	Auto-covariate weighted by estimated larval connectivity to reefs with COTS present	Num	-	(Dormann et al. 2007, Hock et al. 2017)	

4.3.5 Model Fitting

Boosted regression trees (BRT) were used to fit our candidate predictors set to COTS observation data. BRT is a machine learning algorithm that uses many simple decision trees to iteratively boost the predictive performance of the final models (Elith, Leathwick, & Hastie, 2008). Model settings include the learning rate (lr) that controls the contribution of each tree to the final model and tree complexity (tc) that determines the extent to which interactions were fitted. The number of trees that achieved minimal predictive deviance (i.e., the loss in predictive performance due to a suboptimal model) was determined using cross-validation (Elith et al., 2008) (function gbm.step with tc = 3, lr = 0.001, bag fraction = 0.5). Multicollinearity was assessed between candidate variables, however none were omitted with Pearson's correlation values <0.7 (Figure S 9.2). To investigate the effect of spatial autocorrelation and the utility of connectivity- and distance-based auto-covariates, each BRT was fitted to our three response variables (Presence, Prevalence and Outbreak) 3 times: 1) with no auto-covariate; 2) with the spatial auto-covariate ; 3) with the connectivity auto-covariate, to give a total of 9 BRT models. One of the useful outputs of BRT is the relative influence (variable importance, in %) each predictor had in the classification process, allowing each predictor to be ranked in terms of their utility in predicting presence, prevalence or outbreaks of COTS.

Generalised additive models (GAM) were also fit using the same candidate predictor set to potentially identify more parsimonious models. GAM provide a flexible middle ground between traditional generalized linear model models and machine learning approaches. All potential combinations of variables were fitted in a full subsets theoretic approach (Burnham and Anderson 2002) restricting the GAM to include a maximum of 6 variables and maximum 5 knots per variable (n models = 40,815). Full subset models were fitted to each of our three responses in the same categories as the BRT: 1) with no auto-covariate; 2) with the spatial auto-covariate; 3) with the connectivity auto-covariate, for a total of 9 GAM model categories. Each of the variables were then assigned a relative importance indicating the frequency of their inclusion in best-fit models (Fisher et al. 2018) . From the full subset of models for each of the

9 model categories the single best performing model was chosen via Bayesian Information Criterion (BIC). Partial dependency plots (which reveal the effect of a variable on the response after accounting for the average effects of all other variables (Elith et al. 2008)) were produced for the top four most influential predictors for both BRT and GAM models, to investigate the effects of predictors independently. BRT and GAM models were fitted and validated in R 3.5.3 (R Development Core Team 2017) using the "gbm" and "FSSgam" packages respectively.

4.3.6 Model Validation

Each of the 9 BRT and 9 GAM models were subsequently validated against the independent test data and using 10-fold cross validation to estimate prediction accuracy. Validation statistics were combined to produce a single validation metric V_m, calculated for the mth model as:

$$V_m = \frac{DE_m + (CV.ACC_m) + (IND.ACC_m)}{3} \quad [1]$$

where DE is the proportion of deviance explained; CV.ACC is the 10-fold cross-validation accuracy and IND.ACC is accuracy when validated against the AIMS Long Term Monitoring Program dataset. For binary response variables (presence, outbreak), accuracy refers to the proportion of validation observations that were correctly classified, assuming a 0.5 threshold, for gaussian responses (prevalence), accuracy refers to the mean prediction accuracy (1 – mean prediction error).

4.3.7 Ensemble Prediction

The boosted regression tree and generalized additive models for each response were then combined to form weighted ensemble predictions based on the method below (Marmion et al. 2009):

$$WA_i = \frac{\sum_m (V_m \times PRED_{m_i})}{\sum_m V_m} \quad [2]$$

Where WA_i is the weighted ensemble prediction for the *i*th location, $PRED_{m_i}$ is the *i*th prediction for model *m*, and V_m is the validation statistic for model *m* (eqn. 2).

A second ensemble approach was also made by "stacking" the predictions from all boosted regression tree and GAMs into a final boosted regression tree model (Wolpert 1992, Ting and Witten 1999). This is a machine learning approach to ensembles, allowing the boosted regression tree algorithm to choose which model predictions are the most useful in explaining the response variable. The weighted and "stacked" ensemble were then validated against an independent dataset (AIMS Long Term Monitoring Program) to test the generalisability of the two approaches. Final predictions were then made across all reef locations on the GBR using the best performing ensemble model to indicate the reefs most suitable to COTS presence, prevalence and outbreaks.

4.4 Results

4.4.1 Presence Model

Presence of COTS individuals on a reef was best explained by the model containing no auto-covariate model for both BRT and GAM approaches according to both model fit (68.5 and 61.8% deviance explained respectively) and validation against independent data (78.8% and 71.7% accuracy respectively) (Table 4.2). For the best fitting BRT, mean annual exposure to degree heating weeks (DHW_EXP = 13.1% relative influence); exposure to chlorophyll-rich secondary plumes (Secondary = 13.0 %) and minimum sea surface temperature (SST_MIN = 10.8%) were the most influential predictors (Figure 4.2a). Partial dependency plots indicated

a strong negative threshold response at ~1.1 DHW/year and minimum sea surface temperature of ~24°C. Conversely, increasing variability in chlorophyll concentration (CHL_SD) had a relatively linear positive effect of COTS presence, while the frequency of exposure to secondary plumes variables and COTS presence indicated a positive threshold type response at low levels, highlighting the importance of availability of larval nutrition for the establishment of COTS populations.

For GAM models, exposure to cyclonic waves (included in 96.0% of top performing models), primary flood plume exposure (WQ_1 = 92.8%), variation in chlorophyll concentration (CHL_SD = 87.9%) were the most important predictors, followed by average nitrate concentration (NO3_AV = 20.4%) and minimum temperature (SST_MIN = 11.4%). Marginal effects plots of the top performing model reveal a strong positive relationship of both chlorophyll variability (CHL_SD) and in-strength (IN_STR) on the probability of COTS presence (Figure 4.3b). Exposure to primary flood plumes (WQ_1) indicated high probabilities of COTS presence in the absence of primary plumes and a severe dip at low levels before dramatically dropping off again at high exposure to these turbid flood plumes. This finding was relatively consistent for reefs either open or closed to fishing, although sample size was low at the upper extremes of primary flood plumes. Interestingly, cyclonic wave exposure (CYC_EXP) had a generally positive relationship with COTS presence, with a major dip apparent in closed fishing sites, however the confidence limits overlap substantially.

Table 4.2 Validation metrics for each model and ensemble for each of the three response variables; Presence, Outbreaks and Prevalence. Models presented in bold represent the best performing model for each response and model framework. * Accuracy for prevalence is calculated as 1-mean prediction error.

Response	Framework	Model	DE	CV.ACC*	IND.ACC*	Vm
Presence	BRT	PA	0.68	0.87	0.79	0.78
		$PA_{AC.Dist}$	0.68	0.87	0.75	0.77
		$PA_{AC.Conn}$	0.66	0.85	0.74	0.75
	GAM	PA	0.62	0.84	0.72	0.73
		$PA_{AC.Dist}$	0.58	0.83	0.73	0.71
		$PA_{AC.Conn}$	0.62	0.84	0.72	0.73
	ENSEMBLE	Weighted	NA	0.93	0.72	-
		Stacked	0.86	0.96	0.73	-
Prevalence	BRT	PREV	0.85	0.85	0.87	0.86
		$PREV_{AC.Dist}$	0.80	0.85	0.89	0.84
		$PREV_{AC.Conn}$	0.88	0.85	0.88	0.87
	GAM	PREV	0.59	0.84	0.85	0.75
		$PREV_{AC.Dist}$	0.67	0.85	0.87	0.79
		$PREV_{AC.Conn}$	0.57	0.83	0.85	0.75
	ENSEMBLE	Weighted	NA	0.89	0.87	-
		Stacked	0.9192	0.94	0.86	-
Outbreak	BRT	OUT	0.75	0.85	0.77	0.79
		$OUT_{AC.Dist}$	0.74	0.87	0.77	0.79
		$OUT_{AC.Conn}$	0.77	0.86	0.78	0.80
	GAM	OUT	0.61	0.81	0.71	0.70
		$OUT_{AC.Dist}$	0.65	0.82	0.75	0.76
		$OUT_{AC.Conn}$	0.61	0.82	0.71	0.71
	ENSEMBLE	Weighted	NA	0.94	0.77	-
		Stacked	0.87	0.97	0.80	-

4.4.2 Outbreak Model

The outbreak potential of a reef was best explained by the connectivity based auto-covariate model according to both model fit (76.6% deviance explained) and validation with independent data (78.0% accuracy) for BRT. Importantly, the connectivity derived auto-covariate was by far the most influential predictor (AC_CONN = 22.7% variable importance) exhibiting a strong positive effect outbreak potential (Figure 4.2c). Cyclonic wave exposure (8.0% - Negative relationship), minimum sea surface temperature (8.0% - negative relationship), secondary (7.4% - threshold positive relationship) and primary flood plume exposure (6.8% - positive relationship) were also relatively useful predictors of COTS outbreak potential.

GAM models performed best when including the distance based auto-covariate (64.9% deviance explained; 75.6% independent validation accuracy). The distance based auto-covariate (AC_DIST = included in 98.7% of top performing models), bed-sheer stress (wave exposure proxy) (STRESS = 95.9%), exposure to cyclonic waves (CYC_EXP = 94.7%) were the most reliable variables, with exposure to secondary flood plumes (WQ_2 = 53.5%) and estimated maximum coral cover (HC_MAX = 30.9%) also included in a large portion of top performing models (Figure 4.3c). Although models containing the distance based auto covariate outperformed the larval connectivity auto-covariate, the in-strength of a reef was included in a large portion of top performing models (IN_STR = 51.3%). Similarly, marginal effects plots for the top performing model reveal a strong positive relationship for the distance auto-covariate, however the sharper increase suggests that reaching outbreak densities is easier than establishing a truly pervasive population. Outbreaks appear to occur most frequently at reefs that have experienced lower levels of cyclone exposure, however there is another increase in outbreak probability at the maximum levels of exposure. COTS outbreaks also occur at low to moderate exposure to primary flood plumes. Interestingly, there is a sharp increase in the probability of outbreak at relatively low levels of in-strength (i.e. potential larval supply) for

reefs closed to fishing, whereas reefs open to fishing have high chances of having COTS outbreaks regardless of their larval supply.

4.4.3 Prevalence Model

In contrast to COTS presence, the prevalence of COTS populations on a reef was best explained by the connectivity-based auto-covariate model according to both model fit (89.8 % deviance explained) and 10 fold cross validation (14.9 % mean prediction error) for BRT models (Table 4.2). Predictions for COTS prevalence were dominated by water quality variables (CHL_SD = 12.6%; WQ_2 = 8.2%; CHL_AV = 8.0%, WQ_1 = 7.4%) as well as the connectivity auto-covariate (AC_CONN = 7.4%) and exposure to bleaching events (BL_EXP = 6.5%). Inspection of the partial dependency plots indicates generally positive relationships for each of the nutrient related variables (Figure 4.2d). Again, benthic community type (BENT_CL = 0.55%), latitudinal sector (SECTOR = 0.21%) and zoning (ZONE = 0.42%) were poor predictors of COTS prevalence across a reef.

For GAM models using the distance based auto-covariate yielded the best results for model fit (66.7% deviance explained) and validation against independent data (86.6% accuracy). The distance based auto-covariate (AC_DIST included in 98.4% of top performing models), bed sheer stress (wave exposure proxy) (STRESS = 98.0%), exposure to cyclonic waves (CYC_EXP = 49.6%) were the most reliable variables, followed by zoning (ZONE = 26.5%), exposure to secondary (WQ_2 = 25.9%) and primary (WQ_2 = 11.8%) flood plumes. As for outbreaks, although models containing the distance based auto covariate outperformed the larval connectivity auto-covariate, 88.1% of top-performing models included the in-strength (IN_STR) of a reef. Marginal effects plots of the top performing GAM model reveal strong positive effects of both the distance-based auto-covariate and the in-strength of a reef with a negative effect of bed sheer stress and a parabolic relationship with cyclone exposure, with prevalence increasing at higher levels of exposure (Figure 4.3d).

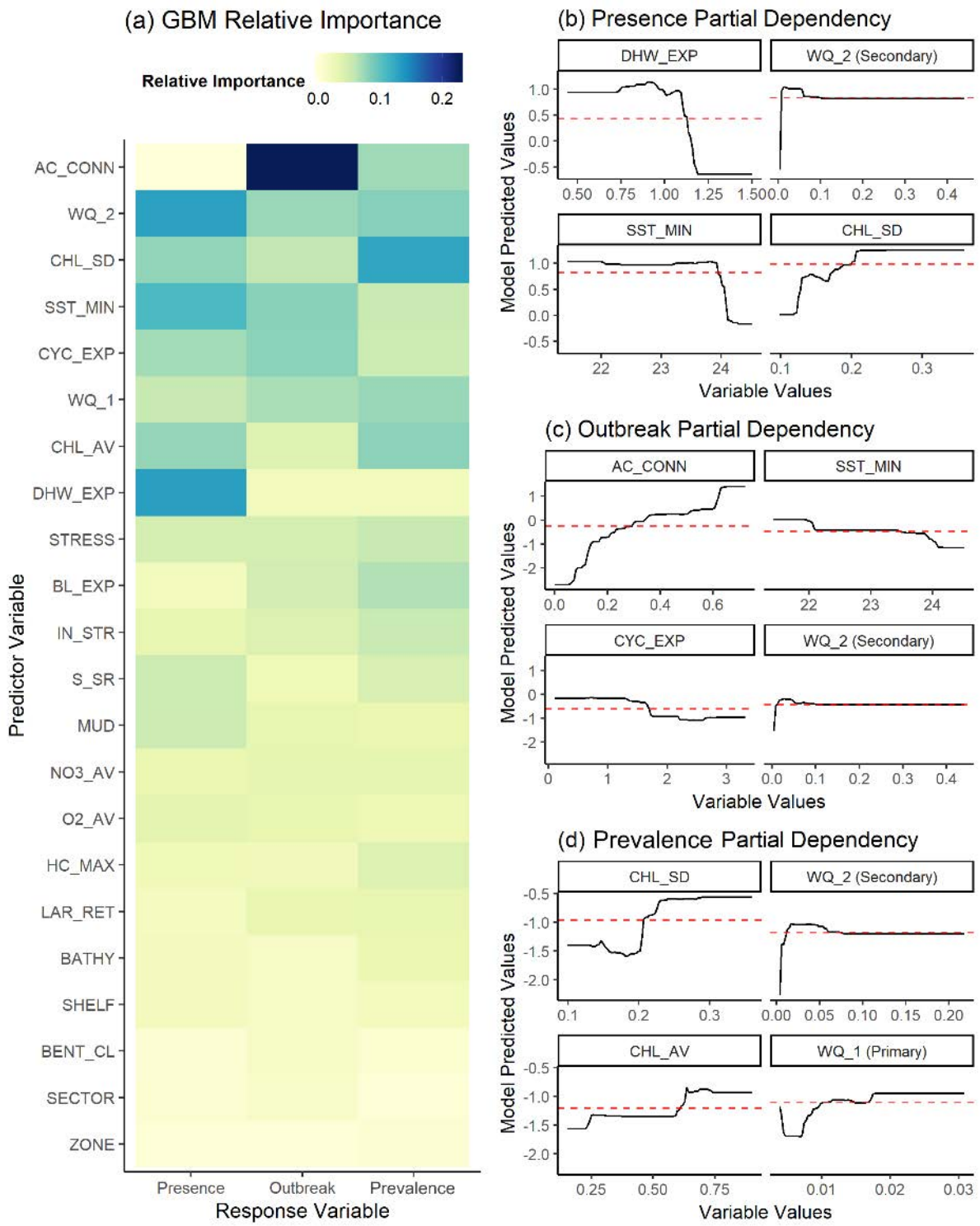

Figure 4.2 Proportion relative importance (Left hand side) (a) and partial dependency plots of the four most influential variables (Right hand side) for best fit boosted regression tree models of COTS Presence (b), Outbreak (c) and Prevalence (d). Best fit models (Table 4.2) are presented for each COTS response variable.

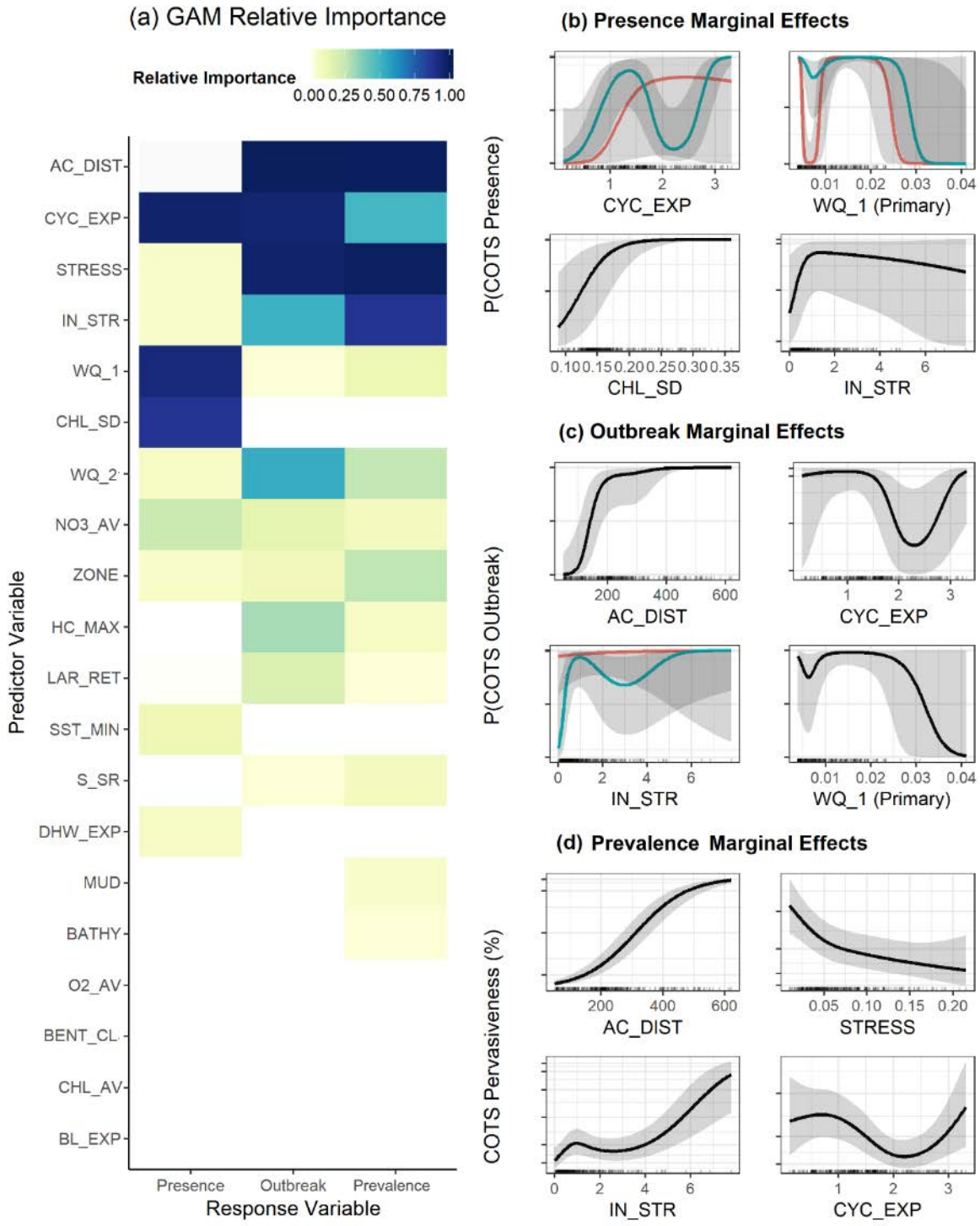

Figure 4.3 Proportion relative importance (a) and marginal effects plots of the four most influential (Right hand side) for best fit Generalized Additive models of COTS Presence (b), Outbreak (c), and Prevalence (d) . Variables with no coloration were not used in any of the best fit models as per the FSSgam procedure. For models including an interaction with zoning, red lines represent reefs closed to fishing and green lines are those that are open for

fishing. NB The partial dependencies shows the single best fit model. The single best fit model does not necessarily include the all the top predictors.

4.4.4 Ensemble Predictions

Ensemble predictions were made for each of the three response variables by combining predictions from all six models (three GAM, three BRT) into both a validation-weighted and a stacked ensemble (Figure 4.4). While dramatically improving model fit and accuracy with the training data, the stacked ensemble method did not improve the accuracy of predictions made by the either best fit model alone or the weighted ensemble approach for the validation dataset (Table 4.2). For binary outcomes validated classification was more prone to Type II errors (Presence: false negative rate = 0.31; Outbreak: false negative rate = 0.30) than Type I errors (Presence: false positive rate = 0.21; Outbreak: false positive rate = 0.15).

Whilst the upper limits of each of the response variables are generally located in the Swains reefs of the Southern GBR and mid-shelf reef of the Central GBR, distinct spatial patterns are observable for each response. Interestingly, relatively high probabilities (>0.5) of COTS presence were predicted offshore of the Whitsundays and Mackay Regions, where little empirical data exists (Figure 4.4a). While COTS may be present along inshore reefs (Figure 4.4), our results highlight that these regions are not suitable for COTS outbreaks or pervasive populations. Interestingly, although a number of reefs in the central northern region of the GBR

are predicted to be suitable for COTS outbreaks, few in this region are predicted to have high levels of prevalence.

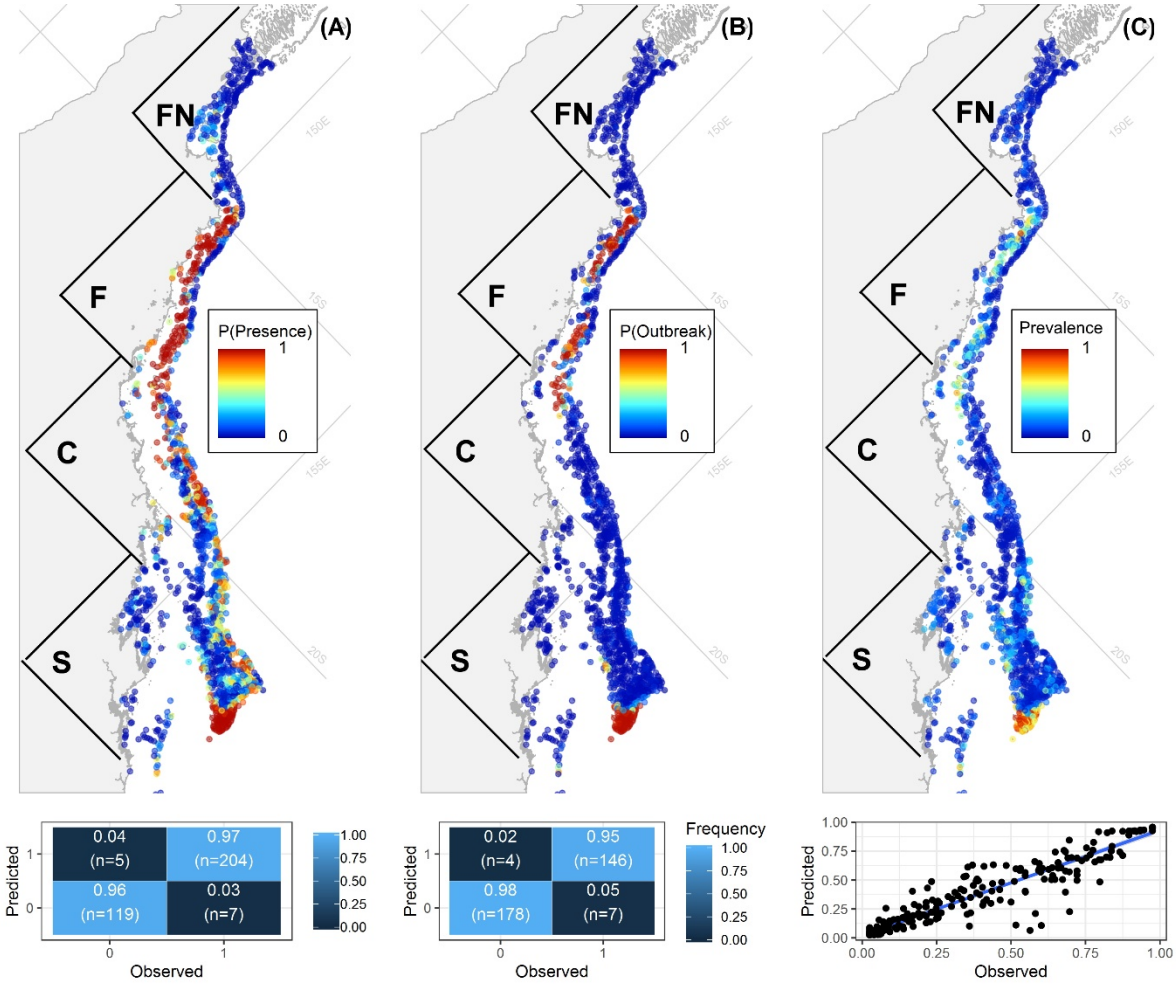

Figure 4.4 Stacked ensemble predictions and cross-validation for COTS presence (a), outbreaks (b) and prevalence (c) across the management areas of the GBRMP (FN=Far Northern, N= Northern, C=Central, S=Southern. Validation statistics are presented as a confusion matrix for presence and outbreaks (0.5 classification threshold) and as linear regression for prevalence.

Ensemble predictions estimate that at the GBR scale, 32% of reefs are suitable for COTS (>50% probability), whilst 12% are susceptible to outbreaks of COTS (>0.22 COTS/Manta Tow) and only 7% are likely to exhibit widespread pervasive population (> 50% tows observing a COTS). There is significant variation among cross-shelf locations and latitudinal

sectors (Figure 4.4), with COTS outbreaks and pervasive populations primarily on mid-shelf reefs in the Southern and Central Northern regions of the GBR (Figure 4.5).

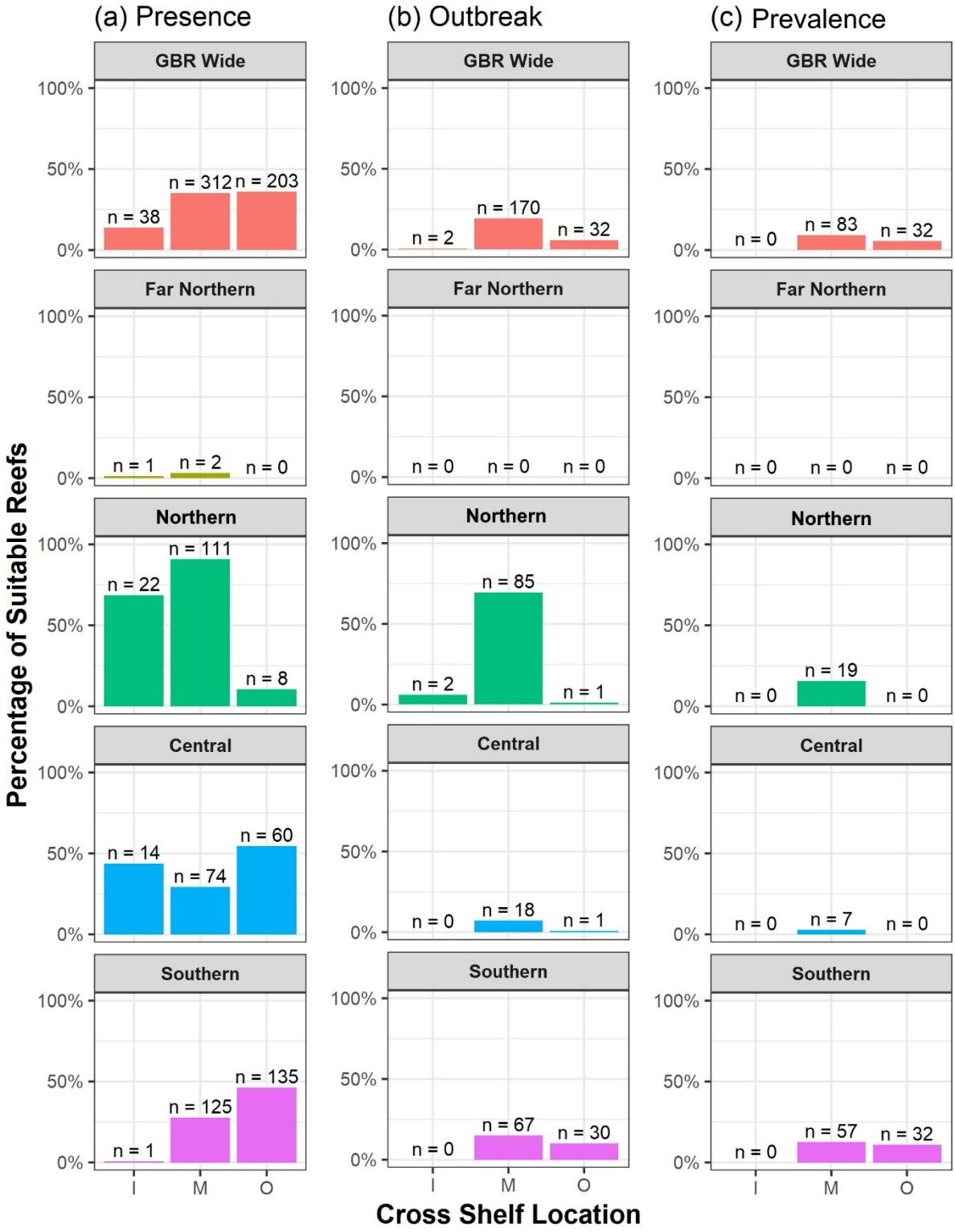

Figure 4.5 Percentage and number of reefs predicted to have COTS presence (b), outbreaks (b) or pervasive COTS populations (c), separated by management sector and cross-shelf location. Predictions use a 0.5 classification threshold to classify whether a reef is subject to COTS presence, outbreaks and pervasive populations

4.5 Discussion

COTS presence, outbreaks and prevalence were explained, to varying degrees, by larval connectivity, water quality, and wave exposure (cyclonic and bed shear stress). For both modelling frameworks, predicting COTS presence on a reef was best achieved by models that did not include the spatial or connectivity based auto-covariate. Importantly however, for COTS to establish secondary outbreaks and/or pervasive populations, our results indicate that there needs to be a substantial larval input from connected reefs, as exemplified by the importance of the connectivity based auto-covariate variables for these responses. Respectively, the connectivity and distance-based auto-covariates act as modelled estimates and proxy indicators of COTS larval supply to a reef, and indeed both have been shown to be equally useful predictors in predicting the probability of an outbreak at a reef (Hock et al. 2014). Together these results indicate that reliable connectivity pathways with COTS source reefs may not necessarily be a prerequisite for COTS presence, as intermittent larval supply may be sufficient to establish low-density COTS populations. However, the establishment of pervasive and/or outbreaking COTS populations are seemingly limited by larval supply from COTS source reefs, with continued propagule pressure promoting COTS outbreak populations above ecologically sustainable levels (Black and Moran 1991, Hock et al. 2014, Pratchett et al. 2017a). These findings add empirical support for larval supply hypotheses and use of connectivity models to predict patterns of COTS secondary outbreaks.

Proxy indicators of water quality (relative flood plume exposure frequency) and larval nutrient supply (annual maximum chlorophyll concentration) had strong positive effects on COTS presence, prevalence and COTS outbreaks. These findings are consistent with larval nutrient supply hypotheses and numerous recent studies highlighting increased larval survival at elevated food concentrations (Uthicke et al. 2015b, Wolfe et al. 2015, 2017, Pratchett et al. 2017b) and correlations between outbreak cycles and chlorophyll-a peaks (Wooldridge and Brodie 2015, Brodie et al. 2017). Particularly important were the results from the BRT models that indicate sharp threshold-type responses at low levels of chlorophyll dominated secondary

plume exposure for all three COTS response variables and a spike in COTS prevalence at ~0.25 and 0.6µg chl-a.L^{-1} (Figure 2c). These results provide some support to the contentious threshold responses to chlorophyll concentrations identified by Fabricius et al (2010), which occur between 0.25 and 1µg chla-a.L^{-1}. Influential positive relationships were also observed for mean and standard deviation of chlorophyll concentration, indicating that both baseline nutrient concentrations (Fabricius et al. 2010, Wolfe et al. 2015, Pratchett et al. 2017b) and exposure to nutrient pulses are indeed important predictors of COTS outbreak dynamics (Wooldridge and Brodie 2015, Brodie et al. 2017). Low levels of exposure to the more turbid primary plumes was an important predictor, particularly for COTS outbreaks and prevalence, yet high levels of exposure appear to be deleterious to COTS populations, presumably due to decreased salinity. Reduced salinity (30% of ambient conditions) has been shown to increase larval survival (Lucas 1973), yet Caballes et al. (Caballes et al. 2017b) observed a sharp decline in fertilization, gastrulation and cleavage rates below 30%, indicating the importance of moderate exposure to plume conditions. These relationships are in accordance with Pratchett et al's (2014) assertion that the spread of outbreaks is conditional on years of high larval survivorship, which is facilitated by major flood events (i.e. infrequent exposure to primary and secondary plumes) that enhance food availability, and promote larval survival. Indeed, our results suggest that regulating water quality on the GBR remains one of the most important management actions for early intervention to reduce or mitigate damage caused by COTS outbreaks.

Most importantly, our results highlight the importance of moving beyond simple (single or dual variable) approaches to modelling COTS distribution patterns. Whilst there is merit in creating easy-to-interpret and parsimonious models, there is an inherent trade-off with model accuracy. For COTS, prediction accuracy is key to determining the allocation of limited resources for COTS control. For example our full model predictions (~95% Accuracy) were far more effective than using solely the potential supply of COTS larvae to a reef (in-strength) (61.1%), exposure to flood plumes (68.1%) or combining both (68.1%). Previous research has used solely simulated connectivity networks to estimate the most important reefs for spreading waves of COTS outbreaks (Hock et al. 2014), planning optimized control procedures (Hock et

al. 2016) and identifying important coral source reefs which could help replenish depleted broodstock (Hock et al. 2017). These estimates of COTS and coral larval dispersal are also used by the GBRMPA to prioritise reefs for COTS control. Our findings do not undermine the utility of these connectivity estimates, but combining them with ecological and environmental parameters can improve predictions of COTS distribution patterns. Moreover, improvements to the underlying assumptions of the connectivity models, particularly the detail of maps (Roelfsema et al. 2018) used to determine reef habitats, and calibration with finer scale hydrodynamic models (Thomas et al. 2014, Bode et al. 2018, Mumby et al. 2018) will further improve modelling estimates and decision-making regarding the allocation of COTS control resources.

One of the most persistent hypotheses to explain the differential occurrence of COTS outbreaks at individual reefs is the 'predator removal hypothesis'. Most studies, however, do not focus on specifically on the abundance of the COTS high profile natural predator (the giant triton, *Charonia tritonis*) due to its scarcity on the GBR, and instead use fishing pressure (i.e. zoning regulation) as a proxy indicator for predator abundance (Sweatman 2008, Vanhatalo et al. 2017). Our study found that zoning regulation was the lowest ranked predictor within the BRT framework, however a few interesting patterns were identified in the GAM models (Figure 4.3b,c). Most significantly was the apparent interaction between potential larval supply (IN_STR) and zoning. The best-fit GAM model indicated low outbreak probability at low levels of larval supply for reefs closed to fishing, but outbreak probabilities remained high at all levels of potential larval supply for reefs open to fishing (Figure 4.3c). This suggests that reefs with lower larval supply may still be able to reach outbreak densities if predation pressure has been reduced. Therefore, our results provide some tentative support for predator-removal hypotheses, however it must be noted that when compared to the importance of other predictors (namely connectivity and water quality) the effect of zoning was small. Furthermore, it must be kept in mind that our analysis, like most other studies, does not account for the effect of the giant triton, as even at pre-harvest densities it is uncertain that they would have been effective at controlling COTS outbreaks (Pearson and Endean 1969, Pratchett et al. 2014). Contemporary

research is aimed at rearing giant tritons and synthesising their predator cues (Hall et al. 2017a, 2017b, Bose et al. 2017) in an attempt to control COTS populations and thus future scenario modelling should aim to identify the potential utility of such approaches.

Understanding and managing for the cumulative impact of disturbance on the GBR, and coral reefs globally, has been a key research objective in recent years (Burke et al. 2011, Hughes et al. 2017a, Mellin et al. 2019a) and our study highlights complex links between disturbance regimes (namely thermal stress and tropical cyclones) and COTS outbreaks. Interestingly, cyclone exposure was an influential predictor for all three responses across both modelling frameworks (Figures 2,3). GAM models revealed interesting marginal effects with a reduction of outbreak, prevalence and presence potential as exposure increased, before an increase at the highest levels of exposure. This can be partially explained by COTS feeding preference for fast growing corals (e.g. *Acroporids, Pocilloporids)* (Pratchett 2007) which are both the most acutely affected by and first to recolonise from severe disturbance events (Mellin et al. 2019b). In this way, recent exposure to damaging cyclonic waves may eliminate COTS preferred food source, yet after some years of recovery, these reefs may become ideal locations for COTS outbreaks. There was a clearer negative trend for wave exposure (i.e. non-cyclonic), indicating COTS preference for more protected mid-shelf reefs, where they are less likely to be disrupted from feeding via oceanic wave action.

In our study, the impact of bleaching and thermal stress was less clear cut, likely because enhanced COTS larval survival in higher temperatures (Uthicke et al. 2015b) competes with the reduction of coral food supply for adults following severe thermal stress events. This means that temperature and thermal stress, whilst being important to COTS life history and prey availability, become difficult to interpret with regards to their effect upon COTS spatial distribution. Exemplifying this, although we found Degree Heating Week exposure and minimum sea surface temperature to be useful predictors of COTS presence (Figure 4.2,3), these more likely represent the latitudinal gradient that exists due to numerous severe outbreaks observed in the southern tip of the GBR and none observed in the warmer, most northern sections. Additionally, there is limited data in the northern region where the greatest impact of

the 2016-2017 mass bleaching events was recorded, making it difficult to draw solid conclusions about the effect of thermal stress and bleaching on COTS. It can be postulated however, that the impact of severe bleaching episodes may be similar to that of tropical cyclones, during which COTS preferred food sources (*Acropora sp.*) experience the most severe mortality (Hughes et al. 2018a), but are also the first to recolonise (Mellin et al. 2019b) given sufficient broodstock remains. Although reefs severely affected by bleaching may not be prone to COTS outbreaks in the short term, it is assumed that if they recover, they will once again become vulnerable to COTS outbreaks. It is important to note that as the incidence of severe bleaching events increases (Hughes et al. 2017b, King et al. 2017), coral cover may decline to a point where no self-sustaining COTS populations can be supported, altering the system entirely.

A few important caveats need to be considered when interpreting our results. Primarily, it is important to note that sampling density plays an influential role in the predictability of COTS distribution patterns. Given that the major predictors of COTS presence, prevalence and outbreaks are were the auto-covariates which relate either the distance or connectivity to reefs with outbreaks, scarce empirical data result in uncertain predictions. For example, high probabilities (>0.5) of COTS presence (Figure 3a) were predicted offshore of the Whitsundays and Mackay (Central-Southern) yet outbreaks or pervasive populations were not predicted in this region. Due to the lack of empirical data in this region, it is unclear if these predictions indicate connectivity between high density outbreak reefs in the Central GBR to the Southern region. It is more likely that our model underestimates the probability of outbreaks and pervasive populations in this region due to the high relative influence of the auto-covariates for these responses. However, as the COTS control program has expanded, there will be unprecedented levels of observational data for the GBR, particularly in the traditionally data poor regions of the far North and Central regions (Figure 4.1). We suggest that as the data from the expanded COTS control program continues to be collected, filling in spatial and temporal gaps, such modelling exercises should be updated to include all available data, or

potentially automated as part of the GBRMPA's planned Reef Integrated Monitoring and Reporting program to keep predictions up to date and continually improving.

Our study is the first to compare the relative influence of these variables alongside a host of other potentially influential factors (i.e. salinity, temperature, wave exposure) on the presence of COTS individuals, the probability of COTS populations reaching outbreak densities and the prevalence of these populations. This highlights the importance of incorporating all available data (namely connectivity and environmental variables) for both the assessment of contemporary theory and also for embedding data into the decision making process. In a time where extensive observational and modelled environmental estimates exist for the entire extent of the GBR and reefs worldwide, it is imperative to build our predictions from all available data and using modelling frameworks that can accommodate them. Given that 30 years of research have not provided a satisfactory simple model to explain spatial patterns of COTS outbreaks (Babcock et al. 2016a, Pratchett et al. 2017a), it is vital to include as much relevant information as possible in our estimates. This study successfully integrates data from multiple disparate sources into a cohesive framework, comparing the relative influence of competing hypotheses for COTS population dynamics whilst also allowing for the nature of individual relationships to be interrogated. Continuing to build data-driven platforms for decision making and embracing emerging technologies for detection will prove crucial to the effective control of COTS on the GBR and globally.

5 Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts

5.1 Abstract

In the face of increasing cumulative effects from human and natural disturbances, sustaining coral reefs will require a deeper understanding of the drivers of coral resilience in space and time. Here we develop a high-resolution, spatially explicit model of coral dynamics on Australia's Great Barrier Reef (GBR). Our model accounts for biological, ecological and environmental processes, as well as spatial variation in water quality and the cumulative effects of coral diseases, bleaching, outbreaks of crown-of-thorns starfish (*Acanthaster* cf. *solaris*), and tropical cyclones. Our projections reconstruct coral cover trajectories between 1996 and 2017 over a total reef area of 14,780 km^2, predicting a mean annual coral loss of -0.67% y^{-1} mostly due to the impact of cyclones, followed by starfish outbreaks and coral bleaching. Coral growth rate was the highest for outer shelf coral communities characterized by digitate and tabulate *Acropora* spp. and exposed to low seasonal variations in salinity and sea surface temperature, and the lowest for inner-shelf communities exposed to reduced water quality. We show that coral resilience (defined as the net effect of resistance and recovery following disturbance) was negatively related to the frequency of river plume conditions, and to reef accessibility to a lesser extent. Surprisingly, reef resilience was substantially lower within no-take marine protected areas, however this difference was mostly driven by the effect of water quality. Our model provides a new validated, spatially explicit platform for identifying the reefs that face the greatest risk of biodiversity loss, and those that have the highest chances to persist under increasing disturbance regimes.

5.2 Introduction

Natural ecosystems are facing unprecedented and accelerating degradation (Ceballos et al. 2015), as exemplified by increasing rates of losses of coral reef biodiversity in the 21st century due to anthropogenic and natural stresses and their interactions (Knowlton 2001, Hughes et al. 2017b). Coral reefs are among the most species rich ecosystems globally (Caley et al. 2014), hosting hundreds of thousands of species (Fisher et al. 2015) and providing important ecosystem services (Costanza et al. 2014). Consequently, the potential impacts of anthropogenic stresses are especially high for coral reef ecosystems.

The resilience of an ecosystem can be defined as its capacity to absorb the impact of a disturbance and return to its initial state (Hughes et al. 2003, 2010, Folke et al. 2004), thereby conferring upon it low vulnerability (Mumby et al. 2014). In this framework, temporal trends in coral cover is the most common indicator of coral reef resilience (Mumby and Anthony 2015), reflecting both its resistance (capacity to withstand disturbance) and recovery (the rate at which coral cover returns to its pre-disturbance level). Threats that undermine coral reef resilience can be broadly grouped into chronic stressors (such as ocean warming, pollution, sedimentation, and over-harvesting) and acute stressors or disturbances (such as coral predation by crown-of-thorns starfish (COTS) *Acanthaster cf. solaris*, coral bleaching, coral disease, and tropical cyclones) that interact in complex ways (Vercelloni et al. 2017). For example, nutrient enhancement from terrestrial runoff can increase coral susceptibility to disease and bleaching (Vega Thurber et al. 2014), and potentially initiate outbreaks of COTS (Fabricius et al. 2010). Herein, 'cumulative disturbance' is used to reflect both the additive and synergistic effects of these acute and chronic stressors. Previous studies have begun to unravel the factors that make a reef more resilient to cumulative disturbance, including herbivory (Hughes et al. 2007b), connectivity (Hughes et al. 2005), and protection from fishing (Mellin et al. 2016a). However, the small percentage of locations where there is regular and detailed data collection represents a bottleneck for understanding resilience at scales relevant to regional conservation and management. Spatial resilience (sensu Cumming et al. (2017)), a subset of the resilience theory,

focuses on processes influencing a system's ability to maintain its integrity and functions that operate across multiple locations and spatial scales, from local (e.g. environmental conditions, habitat characteristics) to regional or global (e.g., management regimes or the impact of regional disturbances exacerbated by global change). Yet there is currently no framework available for predicting which reefs are the most resilient based on spatial variation in underlying environmental, biological, and ecological processes at multiple spatiotemporal scales. Consequently, management plans are routinely designed and implemented with little capacity to quantify their effectiveness in supporting reef resilience, and to improve such plans adaptively.

Australia's Great Barrier Reef (GBR) offers a unique opportunity to disentangle the effects of acute disturbances from the impacts of fishing, which has remained low and well regulated compared to most reefs worldwide. Previous statistical assessments of historical trends for the GBR found a 50% decline in coral cover over the last three decades, mostly due to the effect of cyclones and COTS outbreaks (De'ath et al. 2012). However, those results were based on a subset of 214 reefs, representing 7% of the total reef area of the GBR with few inner-shelf reefs. Furthermore, this assessment did not account for coral recovery following disturbance – a critical requirement for accurately reconstructing coral trajectories and identifying key drivers of reef resilience. Recent advances have helped quantify the effect of cumulative stress on coral recovery potential (Ortiz et al. 2018); however they were based on even fewer samples collected prior to 2010, and consequently, do not include the latest and most severe bleaching events (Hughes et al. 2017b) and recent major cyclone impacts (Puotinen et al. 2016). Only few studies thus far have attempted to identify the environmental drivers of coral growth rate (e.g. Madin et al. 2012, Pratchett et al. 2015, MacNeil et al. 2019) and none has derived high-resolution predictions of coral cover over the entire time series of available data.

Here we develop a high-resolution dynamic model of coral cover for reefs of the GBR that directly incorporates the cumulative effects of disturbances such as coral bleaching, disease, COTS outbreaks, and tropical cyclones. By accounting for key ecological processes (coral growth and recovery potential), environmental drivers of coral cover, and observed disturbance

history, we reconstruct coral cover trajectories for >1,500 reefs at a 0.01° (~1 km) resolution over the last 22 years (1996-2017). Importantly, for the first time our model includes a spatially explicit index of water quality for the frequency of river plume-like conditions (Petus et al. 2014), which can negatively affect corals (Fabricius 2005, Wolff et al. 2018). We independently validate our model predictions and provide quantitative estimates of model uncertainty – a critical requirement for informing decision-making and risk analyses (Mumby et al. 2011). We use this model to map the resilience of corals to anthropogenic and natural stressors across the GBR and show that resilience was negatively related to plume conditions.

5.3 Methods

5.3.1 Experimental design

Model development followed two main steps (Figure 5.1): (*i*) estimate the Gompertz-based model parameters from long-term surveys and predict them in every 0.01° grid cell across the Great Barrier Reef (GBR), and (*ii*) couple these spatially-explicit estimates of coral cover with spatial layers of disturbance history and water quality to reconstruct coral cover trajectories between 1996 and 2017 across the GBR.

Step (*i*) involved predicting benthic communities (i.e. ecological communities composed of hard corals and other benthic organisms or abiotic substrate) based on environmental and spatial correlates using multivariate regression trees. This was done using surveys of average benthic cover for a subset of reefs on the GBR. We then developed a Gompertz-based Bayesian hierarchical model that estimated intrinsic coral growth rate (r_s), as well as the effect of various disturbances on coral cover, for individual transects nested within survey reefs and benthic communities. From these estimates, we predicted intrinsic coral growth rate across the GBR using boosted regression trees (BRT) based on environmental and spatial predictors. We also used our BRT model to predict the coral cover observed in 1996 (HC_{ini}) and maximum (HC_{max}) coral cover in every 0.01° grid cell based on observations at surveyed reefs.

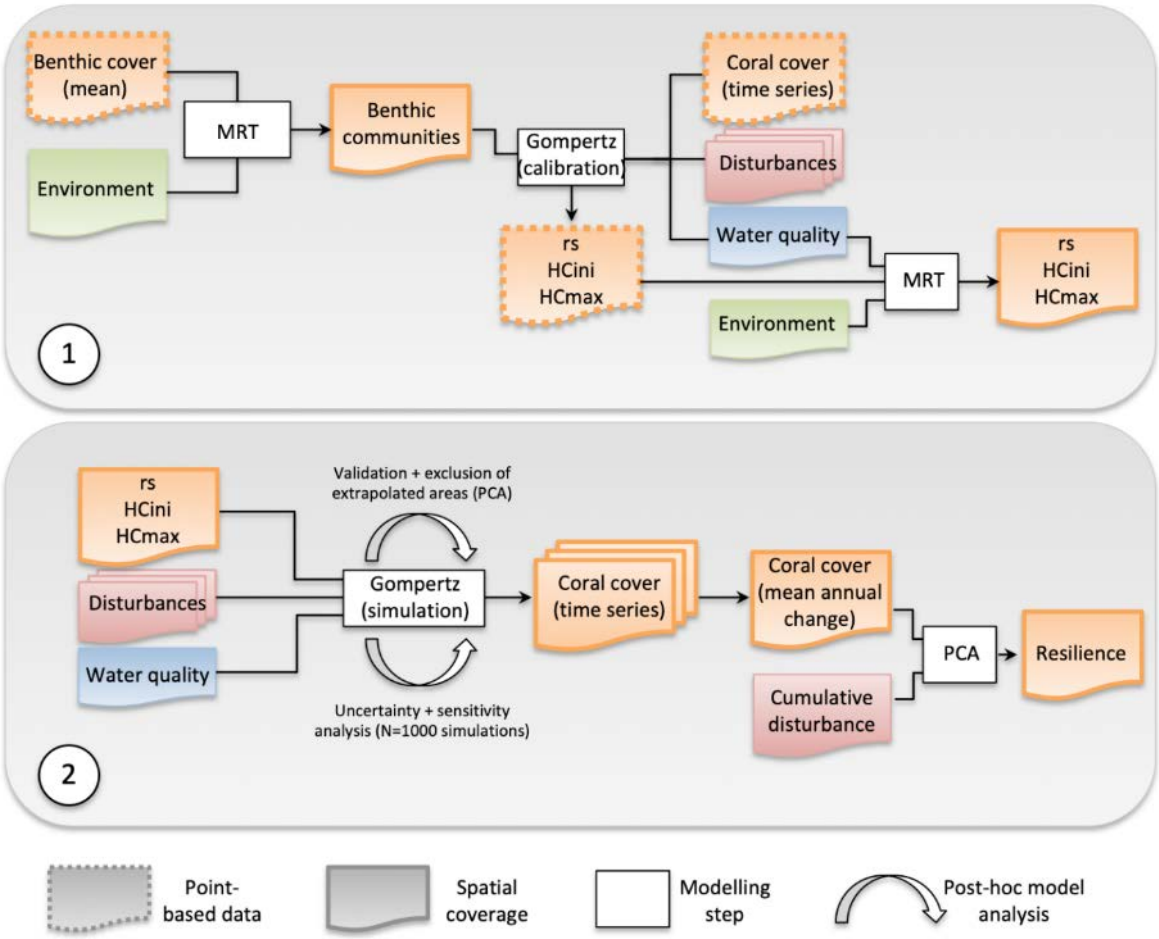

Figure 5.1 Flow chart of the successive steps involved in model development. (1) Benthic communities were predicted across the Great Barrier Reef based on average benthic covers recorded at the survey reefs and environmental covariates using multivariate regression trees (MRT). Initial (HCini), maximal coral cover (HCmax) and coral growth rate (rs) determined from the Gompertz-based model were predicted using boosted regression trees (BRT). In both cases, environmental predictors from Matthews et al (2019) (see

Table S 9.2), in addition to past disturbance history for HCini and HCmax. Survey reefs and sample size used in each step are described in Table S 9.9. (2) The resulting layers were combined with disturbance history recorded for outbreaks of the crown-of-thorns starfish, coral bleaching and tropical cyclones, as well as an index of water quality (i.e. frequency of river plume-like conditions) in the Gompertz-based model of coral growth predicting hard coral cover between 1996-2017, further aggregated over years (coral cover mean annual change). The latter was compared to a cumulative disturbance index to define reef resilience based on a principal component analysis (PCA).

Step (*ii*) involved predicting coral cover in each year of the time series by combining BRT predictions of HC_{ini}, HC_{max} and r_s with the impact (severity × effect size) of the various disturbance agents including coral bleaching, disease, COTS outbreaks, tropical cyclones, and unknown disturbance. This allowed us to predict coral cover in every grid cell and in every year between 1996 and 2017. We validated model predictions using an out-of-sample, independent set of survey reefs, mapped model uncertainty and identified its main sources based on a sensitivity analysis. Last, we compared predictions of mean annual change in coral cover with an index of cumulative disturbance to quantify reef resilience, defined as the net effect of resistance and recovery following disturbance.

5.3.1.1 Survey reefs

Australia's Great Barrier Reef (GBR) consists of more than 3,000 individual reefs extending over 2,300 km between 9 and 24°S latitude. Reef communities of the GBR have been monitored yearly between 1993 and 2005, and then biennially thereafter, by the AIMS LTMP (Sweatman et al. 2008). As part of the AIMS LTMP, a total of 46 reefs were monitored for transect-based benthic cover between 1996 and 2017 in six latitudinal sectors (and management areas) (Cooktown-Lizard Island (Far Northern/Northern), Cairns (Northern), Townsville (Central), Whitsunday (Central/Southern, Swain and Capricorn-Bunker (Southern), see Figure 2.1) spanning 150,000 km^2 of the GBR. In each sector (with the exception of the Swain and Capricorn-Bunker sectors) at least two reefs were sampled in each of three shelf positions (i.e., inner, mid- and outer). An additional 45 reefs were surveyed using the same methodology as part of the Representative Areas Program (RAP)(Sweatman et al. 2008), and 17 reefs as part of the Marine Monitoring Program (MMP) (Thompson et al. 2017). Finally, reef-level

information on hard coral cover was collected by manta-tow for 97 reefs surveyed in 1996 and thereafter (44 of those being also surveyed for transect-based benthic cover).

We used information from the 46 AIMS LTMP reefs in every step of model development, in addition to those from other monitoring programs where possible, depending on the number of survey years and whether associated disturbance data were available (Figure 2.2). We validated coral cover trajectories based on 10 manta-tow reefs that were not used for model calibration, and for which disturbance history as well as ≥10 years of data post-1996 were available.

5.3.1.2 Survey methods and data collection

For AIMS LTMP and RAP, transect-based photograph data on benthic assemblages (broad categories including subcategories: abiotic, hard coral, soft coral, coralline algae, macroalgae, turf algae, sponge, other, indeterminate) were collected at three sites separated by > 50 m within a single habitat on the reef slope (the first stretch of continuous reef on the northeast flank of the reef, excluding vertical drop-offs) (Jonker et al. 2008). Within each site, five permanently marked 50-m long transects (photographs taken at 1m intervals) were deployed parallel to the reef crest, each separated by 10 m along the 6-9 m depth contour. Percent cover of benthic categories were estimated for each transect using point sampling of a randomly selected sequence of 40 (out of 50) images (Jonker et al. 2008). The benthic organisms under five points arranged in a quincunx pattern in each image were identified to the finest taxonomic resolution possible (n = 200 points per transect) and the data were converted to percent cover. For MMP, the smaller size of inshore reefs dictated a reduced design that included two sites at each reef within which five 20-m long transects with n = 160 points per transect were used for estimation of percent cover. In this study, we considered the combined cover of all hard corals, hereafter referred to as hard coral cover (HC; %).

Manta-tow surveys were conducted around the perimeter of entire reefs to estimate hard coral cover and densities of COTS (Miller and Müller 1999). Manta-tow surveys involved a snorkeler with a ‘manta board’ (hydrofoil) being towed slowly behind a small boat around the entire perimeter of each survey reef close to the reef crest so that the observer surveyed a 10-

m-wide swathe of the shallow reef slope (Bass and Miller 1996). The boat stopped every 2 min to allow the observer to record the mean coral cover into one of 10 categories (Bass and Miller 1996), giving one cover estimate per tow (~200 m of reef edge) with the number of tows per reef varying from 3 to 325 depending on reef size.

5.3.1.3 Environmental and spatial covariates

A set of 31 environmental variables were collated across the GBR at a 0.01° resolution (12,670 grid cells, spanning a total area of 14,778 km2) (Matthews et al. 2019). From these variables, we selected those with a reported effect on coral ecophysiology as our candidate model predictors (Table S 9.8). These environmental variables include long term annual averages and seasonal variation of temperature, salinity, chlorophyll a and nutrient concentrations (nitrate, phosphorus), oxygen levels and light availability, as well as sediment covers and bathymetry, which are all important predictors of coral reef and seabed biodiversity on the GBR (Mellin et al. 2010a, Sutcliffe et al. 2014) (Table S 9.8). In addition, spatial variables including the shortest distances to the coast and to the barrier reef were calculated for each grid cell of the GBR using great-circle distance (i.e., the shortest distance between two points on the surface of the Earth). Within this 0.01° resolution grid, reefs (polygons) were identified using the marine bioregion classification from the Great Barrier Marine Park Authority (GBRMPA), excluding any non-reef locations (e.g. cays, islands, mangroves) and restricting coverage to depths <30m. The grid was truncated by removing all cells with a latitude of <12°S due to data scarcity in northernmost locations.

5.3.1.4 Water quality

We used the average frequency of exposure to river plume-like conditions (PFc) as a proxy for exposure to dissolved nutrients and fine sediments delivered during the wet season (MacNeil et al. 2019). Based on satellite observations during the 2005-2013 wet seasons, the frequency (i.e. number of weeks per year) of exposure to primary, secondary and tertiary river plumes were estimated at a 1-km resolution (Petus et al. 2014). Primary water consists of the turbid, sediment dominated parts of the plume, secondary water consists of the chlorophyll-dominated

parts of the plume, and tertiary water consists of the furthest extent of the relatively clearer parts of the plume. Here we pooled these three water types to estimate the frequency of inundation of any plume water, expressed as a proportion of total wet season weeks.

5.3.1.5 Disturbance data

The disturbance data included two components (i) point-based records of coral damage collected concurrently with the benthic surveys (e.g., Mellin et al. 2016a) and (ii) spatial layers of disturbance history and associated severity across the GBR available in Matthews et al. (2019).

(i) In point-based records of coral damage, disturbances were classified into five categories (i.e. coral bleaching, COTS outbreaks, coral disease, cyclones or unknown) following Osborne et al. (2011) based on visual assessment by experienced divers during reef-scale manta tow and intensive SCUBA surveys. A disturbance was recorded when the total coral cover decreased by more than 5% from its pre-disturbance value between two consecutive periods. Each disturbance was identified by distinctive and identifiable effects on corals, such as the presence of COTS individuals or feeding scars, or dislodged and broken coral indicative of cyclone damage (Osborne et al. 2011). An additional category labelled ‘unknown’ was used to classify unidentified disturbances. This dataset thus resulted in a series of five binary variables coding the presence (1) or absence (0) of each type of disturbance in each year and at each reef where transect-based surveys of benthic assemblages were conducted.

(ii) Spatial layers of disturbance severity during the study period were available at a 0.01° resolution for coral bleaching, COTS outbreaks and cyclones (Matthews et al. 2019). In this dataset, per cent coral cover bleached was interpolated using inverse distance weighting (maximum distance = 1°; minimum observations = 3) from extensive aerial surveys at 641 reefs for the 1998, 2002 and 2016 mass bleaching events on the GBR (Berkelmans et al. 2004, Hughes et al. 2017b) Interpolated maps of COTS densities were also generated by inverse distance weighting (maximum distance = 1°; minimum observations = 3) from the manta tow data collected by the Australian Institute of Marine Science in every year from 1996 to 2017

(Miller and Müller 1999). The potential for cyclone damage was estimated based on 4-km resolution reconstructed sea state as per Puotinen et al. (2016). This model predicts the incidence of seas rough enough to severely damage corals (top one-third of wave heights >4m) caused by cyclones for every cyclone between 1996-2016. We then used these spatial layers to associate the binary occurrence of each disturbance resulting in coral cover loss (as per [i]) with its severity. Note that, at the time of writing, aerial surveys following the 2017 bleaching event as well as the impact of the 2017 tropical cyclone Debbie (based on the methodology developed by Puotinen et al. (2016)]) were unavailable. Due to the unavailability of spatially continuous information on the occurrence and severity of coral disease and unidentified disturbance (which both had a low influence on coral cover compared to cyclones or COTS outbreaks), we randomly generated spatial layers for these disturbances in every year and every model simulation (N = 1,000) matching their observed frequency as per the AIMS LTMP historical records.

Disturbance impacts are typically patchy at sub-reef scales, because some sections of the reef might not be exposed to cyclone-generated waves and/or be structurally vulnerable (Puotinen et al. 2016), or because of local COTS aggregation patterns (Pratchett et al., 2014). The consequence is a discrepancy between the expected effect of disturbance from our layers and the actual coral loss recorded at each transect during AIMS LTMP surveys. To explicitly account for such sub-reef scale effects, we resampled the disturbance data in every model simulation (N = 1,000) to match the actual disturbance frequencies observed during field surveys. In other words, we 'turned off' some disturbances assuming they would not result in a noticeable coral loss at the reef scale, with the frequency of these false positives (6.4% for coral bleaching; 6.9% for COTS outbreaks and 9.6% for tropical cyclones) being determined from the AIMS LTMP disturbance history and field-based records of coral loss. We further

assess model sensitivity to the adjusted disturbance data (among other sources of model uncertainty; see Model uncertainty and sensitivity analysis).

5.3.2 Modelling

5.3.2.1 Predicting benthic communities across the GBR

We identified benthic communities using multivariate regression trees (De'ath 2002) (MRT), which allowed us to model the relationship between spatial and environmental covariates, and the relative cover of the different benthic groups and coral taxa. MRT forms clusters of sites by repeated splitting of the data, with each split determined by habitat characteristics (De'ath 2002) and corresponding to a distinct species assemblage. Tree fit is defined by the relative error (RE; total impurity of the final tree divided by the impurity of the original data). RE is an over-optimistic estimate of tree accuracy, which is better estimated from the cross-validated relative error (CVRE). We determined the best tree size (i.e. number of leaves or clusters formed by the tree) as that which minimized CVRE, which varies from zero for a perfect predictor to nearly one for a poor predictor (De'ath 2002). We then examined the splits and quantified the variance that each of them explained, based on the entire dataset and for each individual functional group. We used the resulting MRT to predict community membership for every 0.01° grid cell on the GBR based on the spatial layers available for our covariates. MRT were fit in the R package 'mvpart'.

We subsequently characterized each cluster by its indicator taxa based on the Dufrêne-Legendre index, which is based on the relative abundance and frequency of each benthic category within a given cluster (Dufrêne and Legendre 1997). The index varies between 0, no occurrences of a species within a cluster, to 100, if a species occurs at all sites within the cluster and in no other cluster. The index is associated with the probability of resulting from a random pattern, based on 250 reallocations of sites among clusters (Dufrêne and Legendre 1997).

5.3.2.2 Gompertz model of coral growth

We reconstructed coral cover trajectories over the last 22 years (1996-2017) for every 0.01° grid cell based on the parameters estimated from a Gompertz-based Bayesian hierarchical

model of coral growth previously fitted to the AIMS LTMP reefs (MacNeil et al. 2019). This growth model is an adaptation of the Gompertz-based model of benthic cover developed by Fukaya et al. (2010) that quantifies the intrinsic growth rate (r_s) and strength of density dependence (α) for sessile species, expressed as coverage of a defined sampling area. In our case, this was the percentage of visual points that contained hard coral within the AIMS LTMP data per transect (HC_t). Using a Binomial (BIN) observation model of proportion of hard coral cover (p), we assumed a hierarchy where transect level observations (i) at time (t), were nested within reef (r), nested within each benthic community (c):

$$HC_{crt,i} \sim BIN(100, p_{c,r,t,i})$$

with mean model:

$$\begin{aligned}\log(p_{c,r,t,i} \times 100) &= r_{s,cr} + (1 - \alpha_{c,r})\log(HC_{c,r,t-1,i}) \\ &+ \sum_i \beta_i \, Disturb_{i,t} \\ &+ \sum_i \beta_{i.CA} \, Disturb_{i,t} \times CA_r + \sum_i \beta_{i.PFc} \, Disturb_{i,t} \times PF_{c,r}\end{aligned}$$

[Eq. 1]

and where

$$\alpha_{c,r} \sim N(\alpha_c, \sigma_{\alpha c})$$

$$r_{s,c,r} \sim N(r_{s,c} + k_0 CA_r + k_1 PF_{C,r}, \ \sigma_{rc})$$

$$\alpha_c, r_{s,c}, k_0, k_1, \beta_i \sim N(0, 100)$$

$$\sigma_{\alpha c}, \sigma_{rc} \sim U(0,100)$$

Where r_s is the intrinsic growth rate, α is the strength of density dependence, β_i is the effect size of the ith disturbance occurring in year t ($Disturb_{i,t}$; *i.e.* bleaching, COTS outbreak,

disease, cyclone or unknown), CA is a binary indicating which reefs are located in a closed (i.e. no-take) area, PF_c is the water quality proxy for river plume-like conditions (Petus et al. 2014) and β_{PFc} its effect size, and $\beta_{i.CA}$ and $\beta_{i.PFc}$ are the effect size relating to interactions between disturbances and CA and PF_c respectively. Our model was thus built at a yearly resolution, assuming that any reduction in coral cover measured during a survey (i.e. above the 5% threshold) reflected the impact of a disturbance occurring between that survey and the previous one. We did not include interactions among disturbances because only <1% of all grid cells were affected by two disturbances within the same year, with insufficient instances of AIMS LTMP reefs being exposed to co-occurring disturbances during the study period. Note that in this formulation, each benthic community had their own global mean at the top of the hierarchy.

In the absence of disturbance, coral cover increases from its initial value (HC_{ini}, in 1996 in our case) to its asymptote (HC_{max}, determined by the reef carrying capacity or amount of available substrate in grid cell *i*) where

$$\lim_{t\to\infty} HC_t = \lim_{t\to\infty} HC_{t-1} = HC_{max} \quad \text{[Eq. 2]}$$

which, once combined with Eq. 1, gives

$$\alpha = \frac{r_s}{HC_{max}} \quad \text{[Eq. 3]}$$

Because the strength of density dependence (α) depends on the intrinsic growth rate (r_s) (Fukaya et al. 2010), for which we needed separate predictions in each grid cell, we elected to predict HC_{max} (rather than α) in each grid cell using the same modelling technique to avoid circularity, and calculated α based on Eq. 3.

Those models were run in a Bayesian framework, using the PyMC3 package in Python (Salvatier et al. 2016), with inferences made from 5,000 samples of the default No U-Turn Sampler (NUTS) algorithm. Parallel chains were run, from starting values initialized automatically by an Automatic Differentiation Variational Inference (ADVI) algorithm, to look for convergence of posterior parameter estimates using the Gelman-Rubin convergence

statistic (R-hat); posterior traces and predictive intervals were also examined for evidence of convergence and model fit.

5.3.2.3 Predicting coral growth rate (r_s), initial (HC_{ini}) and maximal (HC_{max}) cover across the GBR

We predicted r_s, HC_{ini} and HC_{max} in each 0.01° grid cell from observed values at the survey reefs and as a function of spatial, environmental and disturbance-based correlates using boosted regression trees (BRT). BRT is a machine learning algorithm that uses many simple decision trees to iteratively boost the predictive performance of the final models (Elith et al. 2008). Model settings include the learning rate (lr) that controls the contribution of each tree to the final model and tree complexity (tc) that determines the extent to which interactions were fitted. The number of trees (nt) that achieved minimal predictive deviance (i.e., the loss in predictive performance due to a suboptimal model) was determined using cross-validation (Elith et al. 2008) (function gbm.step with tc = 2, lr = 0.001, bag fraction = 0.5).

We assumed a Gaussian error distribution in all three BRT, after a logit-transformation of HC_{ini} and $HC_{max}$to achieve normality (no transformation was required for r_s). In addition to spatial and environmental predictors, we used past disturbance history over a 10-year period based on evidence that some disturbance impacts can have temporally-lagged and lasting effects on coral communities over this timeframe (Mellin et al. 2016a). We thus included the mean cyclone severity and the mean COTS density between 1985-1995 to predict the coral cover observed in 1996 (HC_{ini}); and the mean cyclone severity, COTS density during 1996-2016 in addition to the per cent coral bleached in 1998, 2002 and 2016 to predict the maximum coral cover observed between 1996-2017 (HC_{max}). Because r_s estimates already accounted for the influence of past disturbance (filtered out by disturbance parameters in the Bayesian hierarchical model), we only accounted for spatial and environmental variables in this BRT to avoid circularity.

The relative contribution of the predictors to the final models of HC_{ini}, $HC_{max}$and r_s was determined based on the variable importance score (%). For each response variable, the mean

prediction error was assessed using a 10-fold cross-validation (Davison and Hinkley 1997). This bootstrap resampling procedure estimates a mean prediction error for 10 % of observations that were randomly omitted from the calibration dataset; this procedure was iterated 1,000 times. We also verified that model residuals were not spatially autocorrelated using Moran's I and a Bonferroni correction (P > 0.05) (Diggle et al. 1998). Finally, we generated a set of 100 model predictions across the GBR and calculated mean estimates of HC_{ini}, HC_{max} and r_s and their standard deviation in each cell. BRT were fit in R 3.2.2 (R Development Core Team 2017) using the 'gbm' package, along with the tutorial and functions provided in Elith et al. (2008).

5.3.2.4 Correction of systematic bias in manta-tow estimates

To improve model predictive power and spatial representation, we used data from the manta tow surveys (in addition to the transect-based AIMS LTMP data) for calibrating BRT of HC_{ini} and HC_{max} (Table S 9.9). However, due to a moderate yet systematic bias of manta-tow coral cover estimates being lower than transect-based ones (largely resulting from non-coral habitats such as sandy back-reef lagoons being included in the manta tow; Osborne et al., 2011), we first had to derive a corrected manta-tow estimate of coral cover accounting for this bias. We thus fitted a linear regression predicting transect-based coral cover (averaged to the reef level) as a function of manta tow-based coral cover, using data from the 44 reefs that were sampled both by manta-tow and along transects. We then used this regression to predict a corrected estimate of observed coral cover for all reefs surveyed by manta-tow, which we could then compare to transect-based coral cover estimates. For both datasets, we defined initial coral cover at each reef (HC_{ini}) as the mean coral cover observed in 1996 across all transects, and the maximum coral cover (HC_{max}) as the highest mean coral cover observed at that reef between 1996 and 2017.

5.3.2.5 Model validation, uncertainty and sensitivity analysis

We validated predicted coral cover trajectories by comparing them with corrected manta-tow estimates of coral cover for reefs that were not used for model calibration, and for which at least 10 yearly samples were available from 1995 along with the associated disturbance history

(N = 10). Based on these 10 time series, we calculated the mean prediction error (PredErr, %) and the coefficient of determination based on the regression of predictions against observations (R2, %).

We identified areas where model predictions were interpolated (thus resulting in high confidence in model predictions (Leathwick 2009, Yates et al. 2018) and those where predictions were extrapolated (lower confidence). We used a common procedure to identify the environmental envelope used for model calibration based on a principal component analysis (PCA) (e.g., Broennimann et al. 2007, Medley 2010) with environmental and spatial predictors at the survey reefs as input variables, and the 12,670 grid cells as individuals. Based on the PCA individual factorial plan, we outlined the modelled environmental envelope as the convex hull containing all survey reefs. Grid cells falling within this environmental envelope were defined as interpolated locations; conversely, those outside this envelope were considered part of the extrapolation areas.

To account for model uncertainty, we ran a total of 1,000 model simulations in which we resampled every parameter from their predicted distribution. We used Latin hypercube sampling (Norton 2015) (R package 'lhs') to determine a total of 1000 combinations of percentiles, evenly spread out in the new parameter space, which we used to draw a single value forr_s, HC_{ini}, HC_{max} and the disturbance effect sizes (from their posterior distributions) in each simulation. The resulting predictions of coral cover in every grid cell (rows), year (columns) and model simulation were stored as 3D arrays and further aggregated across the third dimension to derive coral cover statistics across model simulations (mean, median, interquartile range and 95% confidence interval). We mapped model uncertainty as the coefficient of variation (%) in predicted mean annual change in coral cover across all simulations.

Finally, we ran a sensitivity analysis to identify, among all model parameters, the main sources of model uncertainty and any possible interactions among them (Pearson et al. 2014). In this analysis, we used the mean annual change in coral cover predicted in each simulation as the

response variable, and the (resampled) parameter estimates used in each simulation as the predictors of a boosted regression tree. This analysis allowed us to quantify the proportion of model uncertainty that is attributable to variation in parameter estimates (i.e., percent deviance explained by the BRT), the respective contribution of each model parameter (i.e., relative importance of each predictor, %) and possible interactions among them (Norton 2015).

5.3.2.6 Mapping coral resilience

We mapped coral resilience (i.e. the net effect of resistance and recovery following disturbance) based on the relationship between predicted mean annual decline in coral cover and cumulative impacts of mean annual disturbance at each reef. To do this, we calculated the cumulative disturbance index in each grid cell as the sum of all cyclones, bleaching and COTS outbreak severities weighted by their respective effect sizes from the Bayesian HLM. We defined categories of low/high decline, and low/high disturbance, based on the median of each index.

We defined resilience as the second axis of a PCA based on predicted decline in coral cover and cumulative disturbance for all reefs (PC2; 21% variation explained). Reefs with relatively low decline following high disturbance (i.e., high resilience reefs) scored positively on PC2, while reefs with high decline following low disturbance (i.e., low resilience reefs) scored negatively. For this analysis, we excluded reefs located in extrapolated areas, for which we had lower confidence in model predictions.

We investigated the relationship between coral resilience and potential anthropogenic covariates that included our water quality index (PF_c), an index of reef accessibility based on potential travel time from nearest human settlement (Maire et al. 2016), and whether a reef was designated as a no-take marine protected area based on the 2004 zoning plan by the Great Barrier Reef Marine Park Authority. We fitted a generalized additive model (Hastie and Tibshirani 1990) to model the relationship between coral resilience and PF_c, and that between resilience and reef accessibility, using a Gaussian error distribution and a cubic spline smoothing function (k=3). We tested whether coral resilience differed among no-take reefs and

those open to fishing using a non-parametric Kruskal-Wallis test. All code was written in R (except for the Gompertz model in Python; see corresponding section) and is provided in Supplementary Information.

5.4 Results

5.4.1 Regional impacts of disturbance on the GBR

The impact of tropical cyclones, COTS outbreaks, and coral bleaching on coral cover varied greatly in space and time across the GBR (Figure 5.2). Based on the 46 reefs regularly surveyed by the AIMS LTMP, our Bayesian hierarchical model showed that tropical cyclones had the strongest, most consistent negative effect on coral cover, followed by COTS outbreaks and coral bleaching (Figure S 9.4). By combining these effect sizes with high-resolution maps of annual disturbance severity, we were able to predict the impacts of each disturbance on coral cover across the GBR from 1996 to 2017 (Figure 5.2a-c) and show regional differences in how these disturbances likely impacted individual reefs.

Cyclone impact was greatest between Townsville and Mackay (Figure 5.2a), where tropical cyclones Hamish (2009) and Dylan (2014) generated some of the longest-lasting destructive waves (Figure 2.2). COTS outbreaks propagated in a southerly direction from reefs north of Cairns (Figure 2.2), and formed a second localised concentration further south. The highest COTS densities on average (and thus the largest COTS impact on coral cover) were recorded off Townsville and on offshore reefs between Mackay and Rockhampton (Figure 5.2b). The impact of coral bleaching, based on aerial surveys following the three mass coral bleaching events (1998, 2002, and 2016), was greatest on the northern half of the GBR (Figure 5.2c), a pattern that was mostly driven by the latest and most severe bleaching event (Figure 2.2).

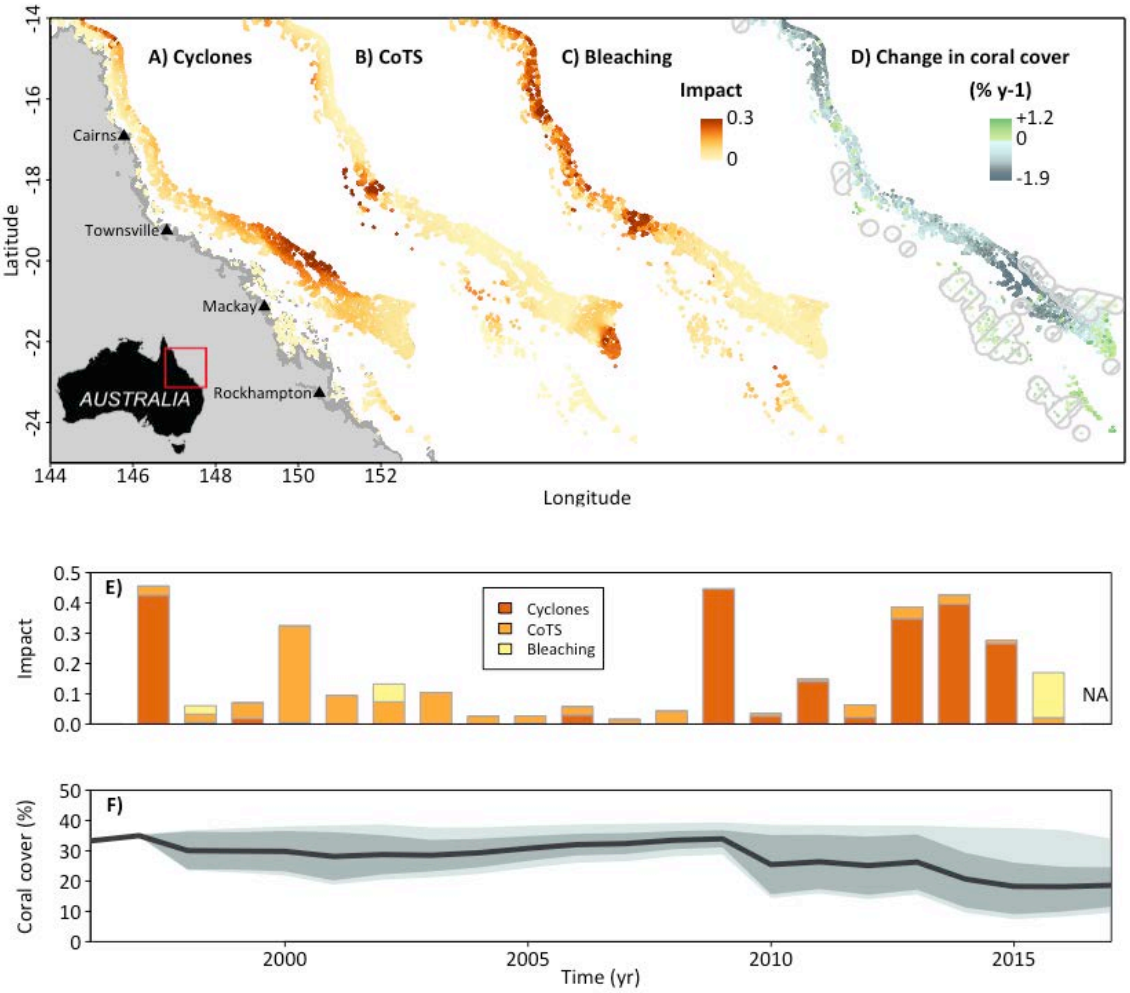

Figure 5.2 Regional impact of major disturbances on the Great Barrier Reef and resulting trends in coral cover. Average 1996-2017 impact of (A) tropical cyclones, (B) outbreaks of the crown-of-thorns starfish (COTS), and (C) coral bleaching (note that only the three mass bleaching events were considered). (D) Mean predicted annual rate of change in coral cover (% y-1) during the same period, with greyed out areas indicating lower confidence in model predictions due to extrapolation. (E) Relative impact of each disturbance in each year. (F) Mean predictions of coral cover averaged across the entire Great Barrier Reef; envelopes indicate the 95% confidence interval across a total of 1000 simulations (light hue), the interquartile range (medium hue) and the mean trajectory (dark continuous line).

Our coral cover predictions closely followed spatiotemporal trends in disturbance impacts, with the greatest decline in coral cover predicted for central reefs mostly impacted by cyclones and, to a lesser extent, northern reefs impacted by both cyclones and bleaching (Figure 5.2d). Between 1996 and 2017, we predicted an increase in coral cover for approximately 10.2% of the total reef area, mostly for southernmost reefs that were less impacted by cyclones and

bleaching (note this calculation excludes reefs for which predictions were extrapolated as this results in low confidence – these areas are enclosed within grey outlines on Figure 5.2d).

Between 1996 and 2017 and across the breadth of the GBR, coral cover declined at a mean annual rate of -0.67% y-1 (Figure 5.2f). This decline was steepest towards the end of the time period (2009-2016; -1.92 % y-1), reflecting a response of hard corals to multiple severe and widespread cyclones (including Hamish in 2009, Yasi in 2011, and Dylan in 2014) and to the 2016 mass coral bleaching event (Figure 5.2e). Coral cover also markedly declined between 1996-2002 (−0.75% y-1), which encompassed mass bleaching events in 1988 and 2002 and a major COTS outbreak (Figure 2.2). In between those time periods, mean coral cover increased by +0.73% y-1 on average (2003-2009).

5.4.2 GBR-wide recovery

Coral recovery potential varied among the different coral communities, which we identified from the survey data and predicted across the GBR using MRT. Among candidate MRT predictors, the distance to the outer barrier reef edge, as well as seasonal variation in sea surface temperature and seabed oxygen concentration (strongly correlated to the latter: Spearman's rho = 0.61, $P < 0.001$) were the main predictors of benthic community composition (Figure S 9.5). Using this model, we were able to define 6 benthic community types across the GBR, which consisted of major functional groups of corals as well as other benthic organisms or abiotic substrate. Outer-shelf communities were characterized by the fast-growing tabular or digitate *Acropora spp.*, as opposed to inner-shelf communities that were characterized by *Porites* or macroalgae (Figure 5.3).

Our Gompertz-based Bayesian hierarchical model revealed that the frequency of river plume conditions (PF_c) had a strong negative effect on coral intrinsic growth rate (r_s), which was higher for outer-shelf communities characterized by tabular or digitate *Acropora* spp. (Supp Fig. S2). Accordingly, high-resolution predictions of r_s derived from the BRT across the GBR

increased from inner- to outer-shelf reefs, with 76% of deviance in r_s posterior estimates explained by the BRT (Figure 5.3a) and a mean cross-validated prediction error of 21 %.

The distance to the reef edge (strongly correlated to PF_c; Spearman's $\rho = 0.63$, $p < 0.001$) was the main predictor of coral growth rate (20% relative importance), followed by the benthic community (10%), and seasonal variation in salinity and sea surface temperature (9% each) (Figure 5.3b). Predicted coral growth rate was the highest for outer-shelf communities characterized by tabulate and digitate *Acropora* spp., and the lowest for inner-shelf communities with relatively high macroalgal cover (Figure 5.3c). The fastest-growing

communities characterized by tabulate and digitate *Acropora* spp. were concentrated in 2.1% of the study area overlapping the outer edge of the GBR (Figure 5.3a).

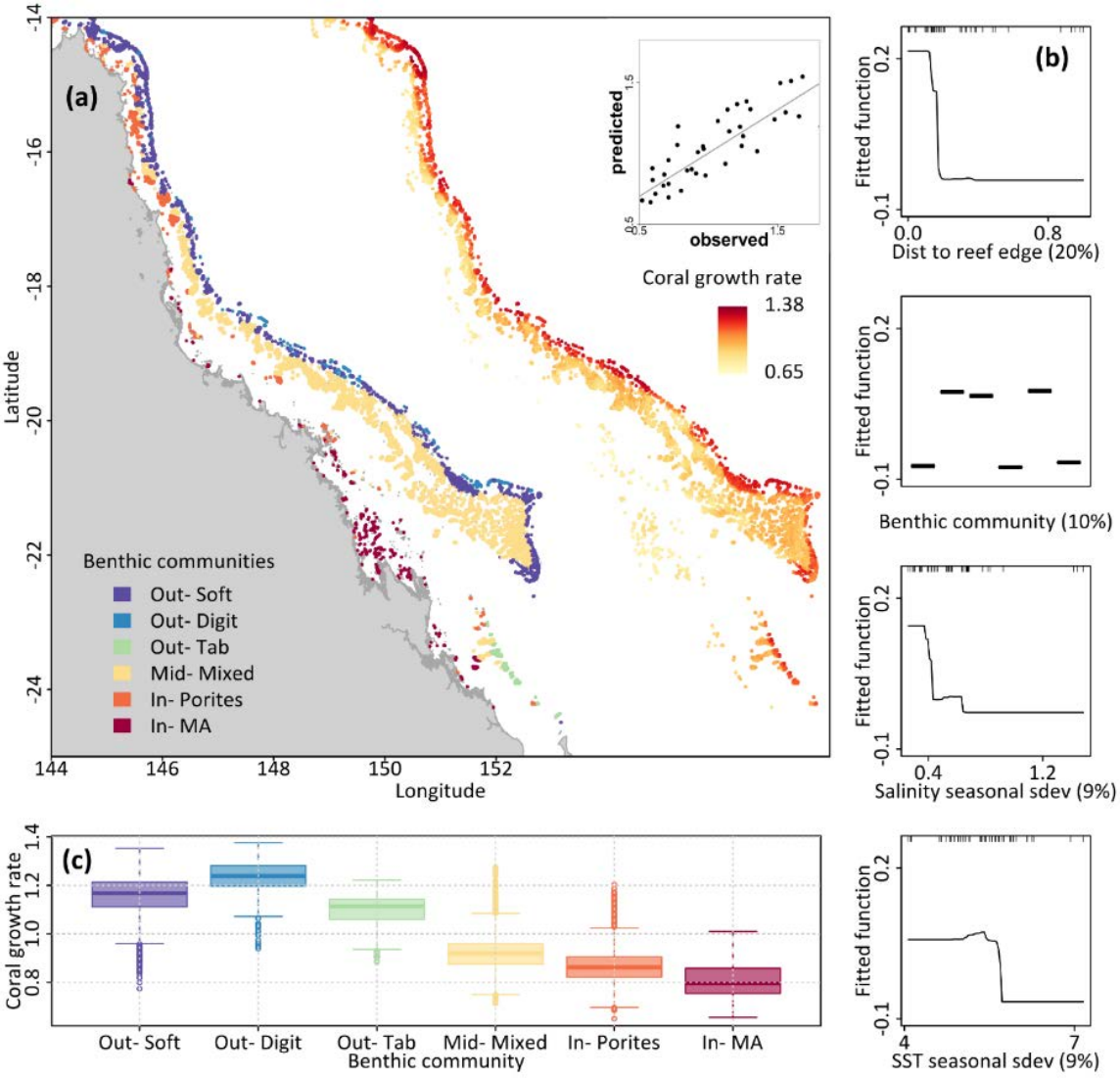

Figure 5.3 GBR-wide predictions of benthic communities and coral intrinsic growth rate. (A) Benthic communities (left) and coral growth rate (right) were predicted based on major environmental covariates using multivariate (MRT) and boosted (BRT) regression trees, respectively. The insert shows the relationship between posterior estimates of coral growth rate from the Gompertz model for the AIMS LTMP reefs, used as observations in the BRT, and BRT predictions. (B) Marginal plots showing the partial effect of major environmental drivers on coral growth rate (with SST = sea surface temperature, sdev = standard deviation). The relative importance of each BRT predictor (%) is indicated in brackets. (C) Distribution of coral growth rate predicted by BRT among benthic communities. The thick line indicates the median, hinges the interquartile range, whiskers the 90% confidence interval and dots the outliers.

Our spatially-explicit predictions of other Gompertz parameters, namely initial (i.e. HC_{ini}, in 1996) and maximum (HC_{max}) coral cover at each reef, showed that BRT explained 78% and 80% of the deviance in HC_{ini} and HC_{max} at survey reefs, respectively (Figure S 9.6). The mean cyclone severity between 1985-1995 had the strongest negative effect on HC_{ini}, followed by

mean seabed temperature. Seasonal variation in salinity was a major driver of HC_{max} at a regional scale, followed by longitude (reflecting cross-shelf environmental gradients in multiple environmental variables that increased or decreased with longitude). Mean cross-validated prediction error was 5% and 11% for initial and maximum cover respectively, with high confidence in predictions within interpolated locations (64% of the study area) (Figure S 9.6).

5.4.3 Mapping coral resilience across the GBR

Based on our cumulative disturbance index that represented the combined impacts of tropical cyclones, COTS outbreaks, and bleaching, most reefs experiencing low disturbance were predicted to show low decline in coral cover, and vice versa (Figure 5.4a). However, 15% of all reefs experienced strong decline following low disturbance, indicating they were low-resilience reefs. Conversely, 17 % of all reefs exhibited low decline following high disturbance, thus representing high-resilience reefs. The latter were mostly located in the southernmost (and northernmost to a lesser extent) sections of the GBR, with a few clusters in the central GBR (dark green on Figure 5.4a).

Reef resilience was strongly and negatively related to the frequency of river plume-like conditions (general additive model; 14.7% deviance explained; Figure 5.4b), and to reef accessibility to a lesser extent (3% deviance explained; Figure 5.4c). When all reefs were considered, reef resilience was substantially lower on closed reefs (i.e. within no-take marine protected areas) compared to open reefs (Kruskal Wallis test; $p < 0.001$) (Figure 5.4d). Most closed reefs were associated with less frequent plume-like conditions (lower median PF_c) than open reefs; however the distribution of PF_c was skewed and resulted in greater mean PF_c within closed reefs (Figure S 9.7). When reefs with greater exposure to plume-like conditions were removed from the analysis, resilience did not differ between closed and open reefs (Figure

5.4d; $PF_c < 0.5$; p = 0.412) although r_s remained substantially higher within closed reefs (Figure S 9.7; $PF_c < 0.5$; $p < 0.001$).

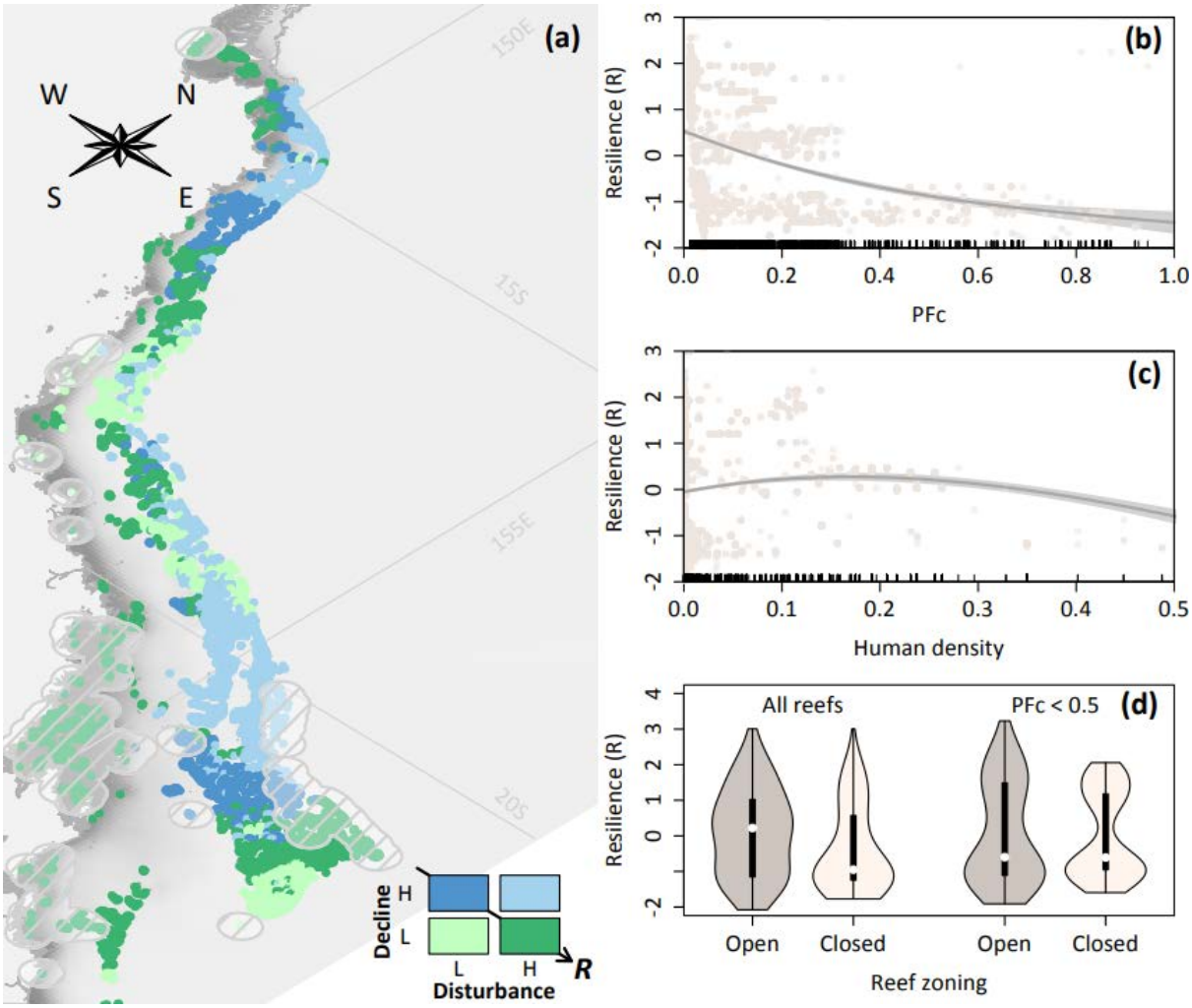

Figure 5.4 Map and correlates of coral resilience on the Great Barrier Reef. (A) Mean annual decline in coral cover vs. mean annual disturbance impact (i.e. the combined severity of all coral bleaching events, COTS outbreaks, and cyclones recorded over the study period, and weighted by their effect size). Low and high categories corresponded to values below and above the median, respectively. High-resilience reefs are characterized by low decline in coral cover following high disturbance, as shown by the resilience gradient (R arrow) used to assign a resilience value to each reef (see Methods). The intensity of the grey shading is proportional to the frequency of river plume-like conditions (PFc). (B) Relationship between coral resilience and PFc. The regression line was fitted using a general additive model (GAM), with the envelope showing the 95% confidence interval. (C) Relationship between coral resilience and reef accessibility (measured as potential travel time from major coastal cities) and GAM fit. (D) Distribution of coral resilience between open and closed (i.e. no-take) reefs, either considering all reefs (left) or only those with less frequent exposure to plume-like conditions (right; PFc < 0.5). The white dot indicates the median, the vertical black bar the interquartile range, and plot width represents the proportion of all reefs.

5.4.4 Model validation, uncertainty and sensitivity analysis

Projected coral trajectories closely matched historical records for 10 reefs surveyed using manta-tow that were not used for model calibration (Figure 5.5). For this independent dataset,

our model accurately captured the impact of multiple disturbances and subsequent coral recovery (mean prediction error = 6.7%; R^2 = 0.57). When considering all reefs with at least 10 years of coral cover data available (N = 54), the mean prediction error was 5.8% and the goodness-of-fit (R^2) was 0.64. Uncertainty in model predictions tended to be higher in the case of rare yet severe disturbances (e.g. Ben Reef; Figure 5.5) compared to multiple, less severe ones (e.g. Credlin or Feather Reefs; Figure 5.5). We mapped the coefficient of variation in predicted annual change in coral cover across all simulations and found that average model uncertainty was 33.6% (ranging 0.7-84.4%). The lowest uncertainty occurred at survey reefs and the highest in central sections of the GBR distant from them (Figure S 9.8).

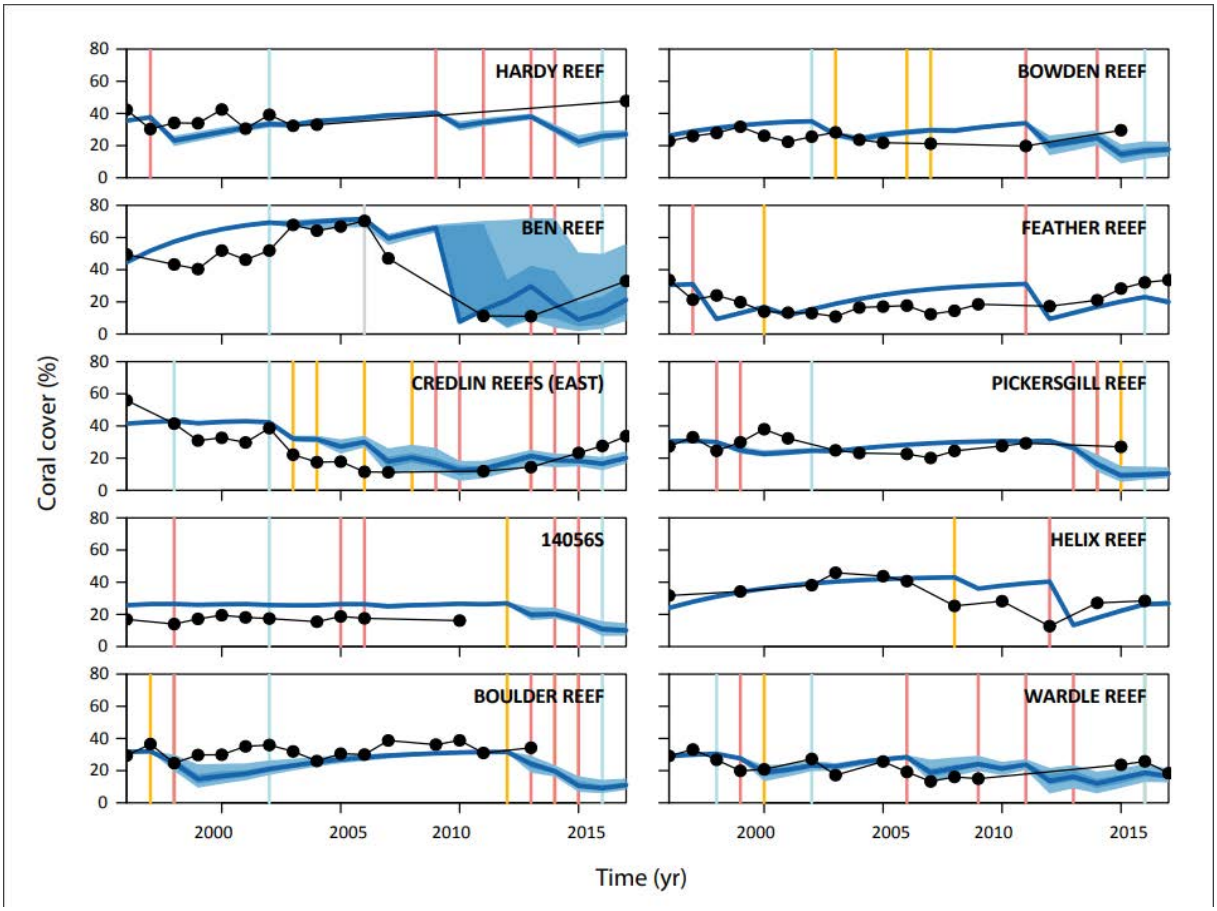

Figure 5.5 Model validation. Predicted trajectories of coral cover (blue envelopes) compared with independent observations (black dots) for manta-tow reefs. Light blue envelopes indicate the 95% confidence interval across 1,000 simulations; medium blue envelopes show the interquartile range (25th and 75th percentiles), and the dark blue line shows the median. Vertical lines indicate disturbances with blue = coral bleaching, orange = crown-of-thorns starfish outbreak, red = tropical cyclone, grey = coral disease.

Our sensitivity analysis revealed that predicted coral decline was the most sensitive to variation in r_s (BRT relative importance = 75%) followed by HC_{ini} (8.9%) and tropical cyclone impact

(4.9%) (Figure S 9.9). We found a weak interactive effect of r_s and HC_{ini} on overall patterns of predicted coral decline, with this effect being greatest at low r_s combined with high HC_{ini} (Figure S 9.9).

5.5 Discussion

By reconstructing coral cover trajectories at a fine spatial resolution across Australia's Great Barrier Reef (GBR) over the last 22 years, we provide the most comprehensive, spatially explicit estimate of long-term coral cover trajectories for any marine system, and disentangle the relative impact of multiple agents of disturbance on coral growth at local-to-regional scales. We show that coral cover is likely to have declined on 90% of all reefs. Historically, this decline has primarily been attributed to tropical cyclones and COTS outbreaks (De'ath et al. 2012), and in more recent years to coral bleaching (Hughes et al. 2017b). High water quality correlates strongly with coral resilience, with low reef accessibility (remoteness) also having a positive, albeit weaker, association. Surprisingly, reef resilience was substantially lower within no-take marine protected areas; however, this difference was driven by the effect of water quality and was not evident among reefs with less frequent exposure to plume-like conditions. We have high confidence in these results because model predictions closely matched independent observation records. By incorporating the main environmental drivers of coral cover and its growth rate into a disturbance-based model of coral decline and recovery, we offer a new and robust framework for similar applications to other reef regions around the world – a critical requirement for sustainable reef management over the coming decades (Hughes et al. 2017b).

Tropical cyclones were the strongest driver of coral cover on the GBR over the last 22 years, which stems from a combination of greater effect size and frequency compared to COTS outbreaks or bleaching. Only a broad-scale and high-resolution approach such as ours that explicitly maps spatial variation across individual reefs could reveal these spatiotemporal patterns, because most of the cyclone impacts occurred within unmonitored reef sections (e.g. Figure 2.2) that were not considered in previous studies (De'ath et al. 2012, Osborne et al. 2017). The stronger effect size of cyclones likely reflects that cyclones typically alter habitat

structural complexity immediately, unlike other disturbances that can leave coral skeletons intact (Osborne et al. 2017). This loss of habitat complexity affects a range of coral-associated organisms such as herbivorous fishes and invertebrates that otherwise facilitate coral recruitment and recovery through grazing (Cheal et al. 2017, Osborne et al. 2017). In contrast, coral cover generally recovers faster following COTS outbreaks because the coral skeletons that remain in place provide suitable habitat for coral recruits and can sometimes shelter remnants of healthy living coral (Osborne et al. 2017).

In our study, the relatively smaller effect of bleaching is partly due to the most severe bleaching event (2016) being only recent (compared to 14 years of cyclone impacts out of a total of 22 years considered), as well as the possibility that some corals might have regained theirs symbionts and recovered by the time AIMS LTMP surveys were conducted. Furthermore, sampling bias might have reduced our estimates of bleaching impacts as we excluded the northernmost reefs (where bleaching impacts were the most severe) due to data paucity, and calibrated our model using observations from the 6-9m depth zone. Corals at these depths might have escaped the most damaging effects of bleaching, which were typically observed on shallow reef flats and crests where low water mixing allowed little cooling from deeper waters (Hughes et al. 2017b). However, such spatial patterns of coral bleaching on shallow reefs are typically patchy (up to a 10-100m scale; S. Heron, unpublished data) and are currently difficult to resolve at the scale of the GBR. Given that coral bleaching is predicted to increase both in frequency and severity over the next decades (Van Hooidonk et al. 2016, Wolff et al. 2018), its impact on coral cover will also likely increase and potentially surpass that of tropical cyclones in the future.

Lower coral resilience coincided with a greater exposure to river plume-like conditions, suggesting that water quality could play an important role in exacerbating the effect of cumulative disturbances and synergies among them. Indeed, chronic stress related to land run-off and poor water quality can affect the functional diversity of benthic communities and result in a loss of resilience (Wolff et al., 2018), potentially aggravating the impact of subsequent acute disturbances (Osborne et al., 2017, Ortiz et al., 2018). Although many indicators of water

quality exist, our results indicate that nutrient and suspended sediment concentrations (as predicted by plume-like water body characterization; Petus et al., 2014) are likely to have a strong negative effect on coral cover and, therefore represent a key management priority (Brodie and Pearson 2016). Conversely, high coral resilience characterized reefs that were previously identified as small and isolated (Mellin et al. 2010b), and thus less prone to deleterious, collateral effects from disturbances at neighbouring reefs. For example, isolated reefs are typically exposed to reduced levels of colonization by COTS larvae (Hock et al., 2014), representing important spatial refugia from outbreaks that tend to propagate along prevailing currents (Pratchett et al. 2014). Identifying the exact drivers of coral resilience warrants further investigation, yet the clear spatial pattern in their distribution suggests that the relative importance of terrestrial influence, cross-shelf location, and spatial connectivity could play a key role in determining coral resilience to multiple disturbances.

Importantly, our study defined resilience as both resistance to and recovery from cumulative disturbance (Hughes et al. 2003, 2010, Folke et al. 2004). While this framework does provide a broader understanding of resilience (as opposed to simply faster growing corals), it does not provide a delineation between the two processes. An important justification of this approach is the time step of the AIMS LTMP surveys used to calibrate and validate the model (1-2 years). In two years, some reefs would have had the time to decline and start recovering, and the absence of surveys in-between means it is impossible to accurately distinguish the resistance from the recovery component. Furthermore, it is important to incorporate resistance as a sub-component of resilience, because greater resistance (i.e. lower impact given similar exposure to disturbance) can sometimes be the main driver of resilience when recovery time are comparable across reef systems (Mellin et al. 2016a). In our study recovery rates (r_s) were characterised amongst benthic community groups and was highest on outer shelf reefs dominated by *Acropora* species. All benthic communities however, were predicted to return to near their estimated maximum (*HCmax)* after ~10 years if unimpeded by disturbance (Figure S 9.4) (MacNeil et al. 2019), suggesting relatively consistent recovery potential among reefs (in terms of return to previous maxima, not annual coral growth rate). While the model predicts

consistent recovery potential and performed well against calibrations and validation datasets, the spatial patchiness of survey data and disturbance impacts mean that predictions are unreliable in some parts of the GBR and uncertainty varies substantially among regions (Figure S 9.8). These limitations highlight that it is important to understand the spatial uncertainty of predictions and also consider the differences between resistance and recovery potential when attempting to predict spatial resilience.

Assessing spatial resilience is an important step toward prioritizing areas for future reef management and conservation, whether the objective is to rescue the weakest or protect the healthiest reefs first (Game et al. 2008). Yet the effect of no-take marine protected areas on reef resilience was strongly determined by water quality, with lower resilience within no-take areas when all reefs were considered. In contrast, when reefs frequently exposed to plume-like conditions were excluded from the analysis, resilience did not differ between no-take or open areas and r_s, our proxy for recovery potential in the absence of disturbance, was higher within no-take areas. This corroborates earlier results suggesting that marine protected areas have the potential to promote reef resistance and recovery following disturbance (Mellin et al. 2016a). The survey design of this earlier study was essentially paired within and outside no-take marine protected areas, with inshore reefs being underrepresented. Another study of inshore reefs found that coral cover was lower within no-take areas than on reefs open to fishing, especially after major flooding events, indicating that repeated exposure to reduced water quality impairs reef recovery following disturbance, regardless of their protection status (Wenger et al. 2016). Together, these results indicate that while no-take marine protected areas have the potential to promote reef resilience due to increased intrinsic growth rate of corals, this potential might not suffice to counteract the deleterious effect of frequent plume-like conditions on reef resilience, suggesting that the location and environmental context of marine protected areas strongly determine their net benefit in terms of resilience.

Assessing the spatial resilience of the GBR has so far remained elusive and understandably ignored in the design of protective zoning. The southern region of the GBR, where we identified most high-resilience reefs, was previously predicted to act as a spatial refuge that

will experience warming later than other coral reefs of the GBR and beyond (Van Hooidonk et al. 2013). Such delayed warming in the southern GBR could contribute both to reduced bleaching-induced mortality, and reduced sub-lethal effects of thermal stress that can lead to lower coral growth rates (Osborne et al. 2017), fecundity, and resistance to disease over many years. Furthermore, more gradual warming may allow a shift to more resistant algal symbionts (Day et al. 2008), thus facilitating the selective emergence of more heat tolerant communities (Hughes et al. 2017b). Our finding of greater resilience in some areas of the southern GBR corroborates the potential for opportunities to intervene and enhance coral resilience through the integration of assisted evolution into coral reef restoration elsewhere on the GBR (van Oppen et al. 2017). However, future forecasts predict that even this 'protective' thermal tolerance induced by sub-lethal bleaching events might soon be lost under current climate change (Ainsworth et al. 2016) if the increased frequency of temperature anomalies outpaces the capacity of reefs to acclimatize and adapt to novel climatic conditions. This means that, ultimately, reducing carbon emissions and mitigating global warming represent the only ways to secure reef persistence in the long term (Hughes et al. 2017b).

Environmental gradients accounted for 76% of variation in coral growth rate (the most influential parameter in our coral cover model), indicating that regional scale assessments based on comprehensive environmental data are key to capturing both the drivers and spatial patterns of coral cover decline and recovery. Low seasonal variation in salinity, temperature and oxygen levels were associated with the fastest growing coral communities, characterized by tabulate and digitate Acropora corals among others. This result seems intuitive, given that these taxa are characterized by a 'competitive' life history that can dominate communities in suitable environments, but are also very sensitive to environmental changes such as temperature anomalies (Darling et al. 2012) Temperature gradients are among the main natural drivers of species distributions, affecting somatic growth and body size (Lurgi et al. 2012), and directly reflecting the physiological influence that temperature exerts on individual species (Mellin 2015). Furthermore, the importance of seasonal variation in oxygen levels as a determinant of benthic communities indicates that different taxa respond differently to oxygen

depletion (Pitcher et al. 2012), which can reduce coral calcification rates (Colombo-Pallotta et al. 2010) and appeared strongly temperature dependent in our data. However, modelling coral growth rate across the breadth of the GBR was also greatly improved by including spatial variables (such as the distance to the reef edge) that can provide a proxy for environmental gradients either not considered or poorly estimated (Mellin 2015).

Based on 20 years of data, our model provides a platform for projecting coral cover trajectories under past and future scenarios of climate change, which has and will continue to affect the frequency and severity of coral bleaching (Van Hooidonk et al. 2016), tropical cyclones (Walsh et al. 2016) and COTS outbreaks (Uthicke et al. 2015b). The critical question remains whether and when the capacity of reefs to absorb and recover from disturbances might be outpaced by future changes in these disturbance patterns. Our modelling approach is broadly applicable across reef ecosystems, especially given that relevant environmental and spatial layers are now increasingly available through the routine use of remotely sensed products (Mellin et al. 2009). Our framework thus provides the advance needed to forecast which reefs will remain as important refugia for sustaining coral reef ecosystems under increasing pressures from global change.

6 COTSMod: A spatially explicit metacommunity model for the management of Crown-of-thorns starfish and coral recovery

6.1 Abstract

Outbreaks of the Pacific crown-of-thorns starfish (COTS; *Acanthaster* cf. *solaris*) have been responsible for 40% of the decline in coral cover on the GBR over the last 35 years. With the intensity and frequency of bleaching and cyclonic disturbances predicted to increase, effectively managing these outbreaks may allow reefs an opportunity to recover from these cumulative impacts. Despite significant research surrounding COTS outbreaks, there is currently no framework available to simulate the effect of COTS management action at regional scales. We developed a stage-based metapopulation model for COTS at a 1x1km resolution using long-term time series and modelled estimates of COTS larval connectivity, nutrient concentrations and important vital rates estimated from the literature. We coupled this metapopulation model to an existing spatially explicit model of coral cover growth, disturbance and recovery across the GBR from 1996-2017 to create a metacommunity model. Our results were validated against a spatially and temporally extensive dataset of COTS and coral cover across the GBR, predicting an average coral decline of 1.3% p.a. across the GBR, and accurately recreating coral cover trajectories (mean prediction error = 7.1%) and COTS outbreak classification (accuracy = 80%). Sensitivity analyses revealed that overall model accuracy was most sensitive to larval predation (boosted regression tree; relative importance = 46.7%) and two parameters defining juvenile density dependent mortality (21.5 and 17.5%). The COTS model underestimated peak COTS densities particularly in the Swains and

Townsville sectors of the reef, whilst overestimating COTS density during non-outbreak years. A better understanding of inter-annual variability in larval connectivity, and regionally variable density dependence for adult COTS life stages may improve model fit during these extreme outbreak events. Our model provides a platform upon which the effects of implementing varying combinations of COTS interventions can be simulated, providing guidance for management and researchers as to the most effective management strategies and technologies respectively. These advancements may allow the quantification of the potential gains in coral cover that could be expected under each strategy/technology and provide a vital tool for effectively managing COTS outbreaks and coral recovery at a regional scale.

6.2 Introduction

Crown of thorns starfish (COTS; *Acanthaster* spp.) are a prominent coral predator among coral reefs in the Indo-Pacific. COTS are characterized by an immense fecundity (Kettle and Lucas 1987, Babcock et al. 2016b), combined with synchronous spawning and consequently high fertilization rates (Babcock and Mundy 1992, Babcock et al. 1994), making them predisposed to rapid increases in density, or outbreaks (reaching up to >1,000 individuals ha^{-1})(Chesher 1969, De'ath 2003, Kayal et al. 2012). These factors combined with increased nutrient availability for larval COTS (Brodie et al. 2005), reduced predation on both juvenile and adult life stages (Endean 1969, Sweatman 2008), and favorable hydrodynamic conditions (Hock et al. 2014, Wooldridge and Brodie 2015) are hypothesized to be responsible for the initiation and spread of COTS outbreaks. On the Great Barrier Reef, outbreaks of the COTS are a major cause of coral loss, responsible for ~40% of the coral declines over the last 30 years (De'ath et al. 2012, Mellin et al. 2019a). Also, among the major causes of coral loss (e.g cyclones and bleaching), COTS outbreaks are the only disturbance that may be readily amenable to direct interventions (De'ath et al. 2012). Although outbreaks of COTS has been a key research and management focus (Pratchett et al. 2014, 2017a, Westcott et al. 2016, GBRMPA 2017), there remains considerable uncertainty regarding the exact mechanisms by which COTS outbreaks initiate, spread and halt (Pratchett et al. 2017a) as well as the efficacy of COTS management

more broadly. Creating predictive modelling frameworks that account for such uncertainties are fundamental in improving management of COTS and the desired outcome of protecting coral.

Four major outbreak events have previously been documented on the GBR, beginning in 1969, 1979, 1993 and 2010 (Pratchett et al. 2014). Primary outbreaks are typically initiated on reefs in the northern GBR (Endean 1974, Johnson 1992, Stump 1996, Vanhatalo et al. 2017) and followed by secondary outbreaks that propagate on downstream reefs through the transport of larvae via ocean currents (Endean 1974). Successive outbreak events have occurred roughly 10-17 years apart, with COTS observed at outbreak densities (>0.22 COTS per 2 min manta tow) on individual reefs for 2-5 years depending on the amount of available coral prey and the rate of depletion (Pratchett et al. 2014). Primary outbreaks build up over a number of years within the Northern management region (Figure 6.1: Cairns and Cooktown/Lizard Island sectors) initiated in part by elevated nutrient conditions resulting from riverine input during the wet season, which is hypothesized to dramatically increase the survival of COTS larvae (Brodie et al. 2005, Fabricius et al. 2010, Wolfe et al. 2017). However, elevated nutrient conditions occur quite frequently (3-5 years) in this region and do not always result in primary outbreaks (Wooldridge and Brodie 2015). Wooldridge and Brodie (2015) highlighted how the initiation of primary outbreak occurred when elevated nutrients coincided with increased larval connectivity between reefs during neutral El Niño Southern Oscillation (ENSO) phases. Due to the preference of COTS for fast growing corals (Pratchett et al. 2014), and the relationship between maternal nutrition and fertilization success (Caballes et al. 2016), the time lag between outbreak cycles is also likely linked to the recovery period required for fast growing corals following a COTS outbreak.

Once initiated, secondary outbreaks are generally observed on the mid shelf reefs south of the "initiation box" and are exemplified by large larval influx and more dramatic increases in COTS densities, aided by near-annual nutrient enrichment (Brodie et al. 2017). Primary outbreaks that occur in the southern Swain sector of the GBR were suggested to be somewhat independent from and concurrent with the northern outbreaks (Brodie et al. 2017)(Figure 6.1).

Following an outbreak, COTS populations decline dramatically, often completely absent in surveys the following year (Pratchett 2005b, Sweatman et al. 2008, Vanhatalo et al. 2017). These declines are presumably due to density dependent mortality processes such as starvation or disease (Pratchett 1999), although this process is poorly resolved and has not been well documented in the field or recreated in laboratory conditions (Pratchett et al. 2017a). After populations at a reef collapse, COTS are usually not observed again in significant densities for around 10 years, often allowing coral to recover (pending no other disturbance) before the next outbreak cycle begins (Figure 6.1).

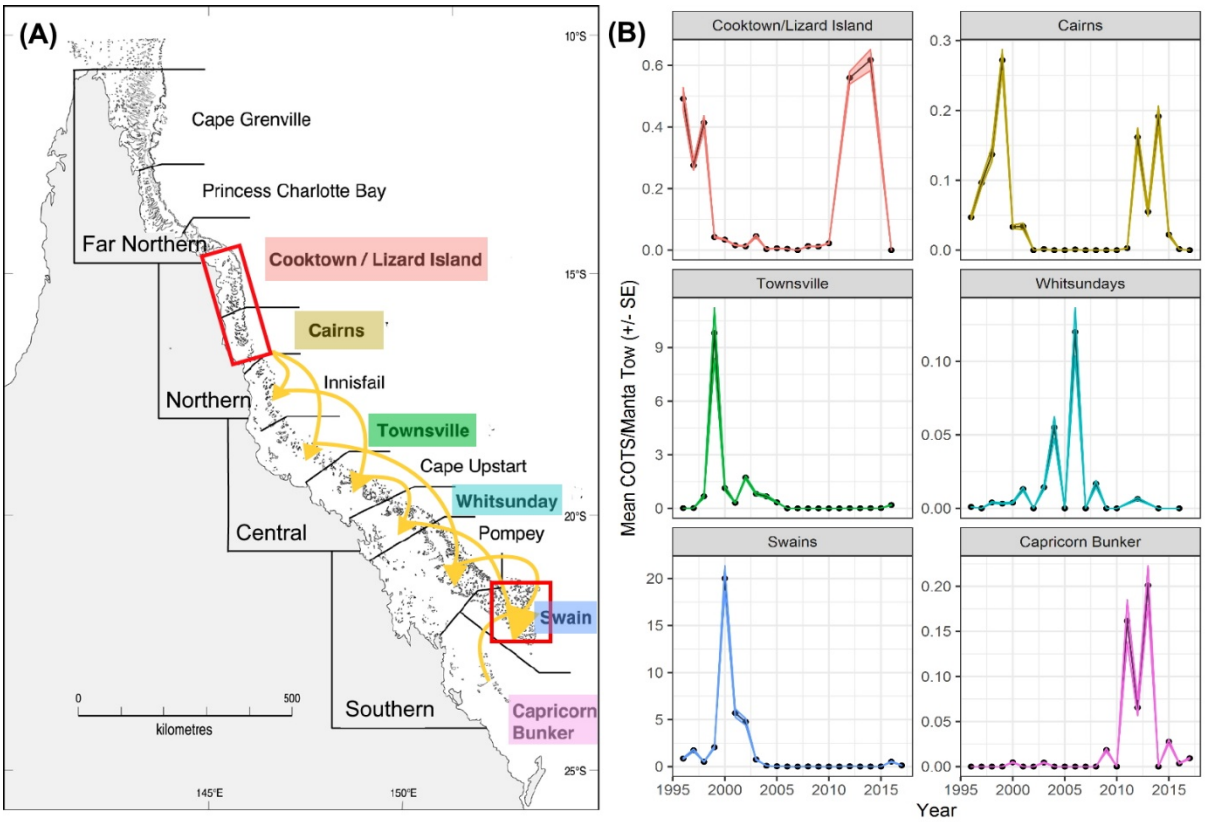

Figure 6.1 a) Representation of initiation zones for primary outbreaks (red boxes) and the subsequent propagation of secondary outbreaks at downstream reefs.b) Empirical estimates of COTS densities aggregated for six major sectors of the GBR from the AIMS Long Term Monitoring Program (AIMS LTMP). Also presented are the four management areas of the GBR.

As outbreaks of COTS represent the only major disturbance amenable to direct action, the Great Barrier Reef Marine Park Authority (GBRMPA) has deployed significant resources into the tactical (short term) and strategic control of COTS on the GBR (Fletcher and Westcott 2016, Westcott et al. 2016). Following the initiation of the current outbreak cycle in 2010-11, the COTS control program operated two vessels primarily in the initiation zone, with resources

being moved further south following the spread of secondary outbreaks. These vessels targeted reefs of high tourism and ecological value experiencing COTS outbreaks, to protect coral assets at a local scale (Westcott et al. 2016). In recent years there has been improvement and expansion of the COTS control program (5 vessels from November 2018) for example using hydrodynamic modelling estimates of COTS and coral larval transport to identify reefs which may be important reefs to protect from a network perspective, to promote recovery (Hock et al. 2014, 2017). Additionally, there have been significant developments in technology for the early detection of COTS outbreaks (Doyle et al. 2017, Uthicke et al. 2018) and some progress in identifying pathways to aggregate or disperse COTS populations for control purposes (Hall et al. 2017a, 2017b). Despite these technological and strategic advancements, there is currently no spatially and temporally explicit modelling framework upon which we can simulate the effect of these emerging management scenarios to understand the potential benefits of alternative COTS management options. Furthermore, there is no consensus on the spatial scales at which COTS control can be effective (Pratchett and Cumming 2019) and under what conditions control may inadvertently promote chronic infestations of COTS by disrupting the boom-bust cycle (Nakamura et al. 2014). Building simulation models at an ecosystem level is therefore a vital step in understanding the positive and negative consequences of interventions of this scale.

COTS rapid expansion in range and boom-bust dynamics during outbreak cycles (Uthicke et al. 2009) mean significant care must be taken when modelling their population dynamics (Mellin et al. 2016b). Density dependent or resource dependent vital rates (e.g. mortality, fecundity) are key parameters for simulating boom and bust dynamics in a demographic population model (Caswell 2006). For COTS, Lokta-Volterra predator prey dynamics (Lotka 1910, Volterra 1928) have traditionally been used to model outbreak cycles (McCallum 1993, Morello et al. 2014, Mellin et al. 2016b), focusing primarily on coral prey availability in determining COTS mortality rates. However, for COTS, it is not apparent that all "bust" phases of the outbreaks are necessarily linked to comprehensive depletion of coral resources (Pratchett 2010), and density-dependent pathogenesis is also hypothesized to play an important role in

COTS population collapse (Zann et al. 1987, Birkeland and Lucas 1990, Pratchett 1999). Ratio-dependent processes, where vital rates are linked to the ratio between available prey and predator abundance (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000, Haque 2009), are an alternative approach to Lotka-Volterra type dynamics, aiming to represent both density and resource dependent processes. Incorporating both predator and prey dependent processes may offer a solution to simulating boom-bust dynamics for COTS, particularly to capture a "bust" mechanism that does not require total resource depletion.

Recent advances in hydrodynamic, COTS population and coral growth modelling were important precursors to the development of a modelling framework for a COTS-Coral metacommunity model at the GBR scale. MacNeil et al. (2019) developed a Gompertz-based coral growth model for reefs monitored by the Australian Institute of Marine Sciences Long Term Monitoring Program (AIMS LTMP). This model was extended by Mellin et al (2019a), who recreated the trajectories of coral cover across the entire GBR at a 1x1km resolution using a dataset defining the disturbance history and environmental characteristics of reef locations (Matthews et al. 2019). Furthermore, significant advances in larval connectivity modelling (Condie et al. 2012, Hock et al. 2014) have allowed connectivity networks for COTS to be derived over four spawning seasons (2012-2016) (Hock et al. 2017), whilst the development of the eReefs biogeochemical model allows estimates of important environmental conditions such as chlorophyll-a concentration to be estimated across the GBR for recent years (Johnson 1992, Chen et al. 2011, CSIRO 2019). Additionally, recent studies have developed population models for COTS at small scales, highlighting the importance of trophic interactions in COTS population dynamics (Morello et al. 2014, Mellin et al. 2016b) and identifying important ecologically relevant thresholds for COTS control above which coral cover is reduced (Babcock et al. 2014) and fertilization rates (Rogers et al. 2017). Combined with the extensive literature surrounding COTS biology outbreaks (reviewed by Caballes and Pratchett 2014, Pratchett et al. 2014, 2017) these advances provide the platform necessary to build a COTS-

Coral metacommunity model that will allow researchers and managers to investigate the likely effect of management actions.

This study builds upon an existing model of coral growth and disturbance across the GBR (Matthews et al. 2019, MacNeil et al. 2019, Mellin et al. 2019a) by incorporating a COTS population model at each reef, linked by larval connectivity estimates (Hock et al. 2014, 2017) to create a COTS-Coral metacommunity model for the GBR at a 1x1km resolution. This study aims to: (1) use the best available data to recreate and validate the trajectories of COTS and coral populations across the entire GBR; (2) investigate which parameters are most important for recreating COTS outbreak patterns, to identify improvements required in our understanding to refine predictions and identify potential strategies that could be targeted by management and (3) provide a platform for future development to compare COTS management strategies. The results of these simulations and the metacommunity platform itself will provide managers a useful tool to direct the allocation of resources for the next outbreak cycle.

6.3 Methods

A COTS-Coral metacommunity model (https://github.com/sammatthews990/COTS_Model) was constructed at a 1x1km resolution to recreate the trajectories of coral and COTS across the GBR between 1996-2017. The metacommunity model framework can be summarized according to four subcomponents: (i) the coral dynamics model governing coral growth and impacts from other disturbances (cyclones, bleaching, disease); (ii) COTS population model recreating the life history and density dependent processes for each 1x1km grid cell; (iii) a larval survival model which controls the proportion of larvae surviving from each spawning event based upon the nutrient conditions, and (iv) the larval connectivity model which disperses COTS larvae among reefs, linking individual reef population into a metapopulation model. COTS populations are initiated in the model using GBR-wide estimates of COTS density in 1996, derived from the AIMS LTMP (Matthews et al. 2019). Model simulations are then run to recreate trajectories between 1996-2017. The model is calibrated to fit manta tow observations for coral cover and COTS for 46 reefs that were surveyed at least 10 times

providing reef-wide estimates of coral cover and COTS densities. Validation statistics were calculated on a further 91 reefs that were surveyed between 5-10 times between 1996-2017.

6.3.1 Coral Dynamics Model

Coral growth was parametrized across a standardized 1x1km grid for reef locations, as defined by a Gompertz-based growth curve (Table 6.1). Previous research defined the growth curves and disturbance coefficients for 47 AIMS LTMP reefs (MacNeil et al. 2019). These growth parameters were then modelled for all reef locations across the GBR based on the predicted coral community composition (Mellin et al. 2019a). At each yearly time step, coral cover was affected by disturbance (cyclones, bleaching, disease) and then recovered as per the spatially explicit estimates for coral growth (Figure 6.2). Annual disturbance exposure for the model was provided from a dataset compiling the disturbance history for the GBR (1986-2017) on the standardized 1x1km grid (Matthews et al. 2019). Although this coral model was originally calibrated to include disturbance from COTS outbreaks as predicted from the AIMS LTMP, in

our framework this portion of the coral dynamics model was replaced in the present study by a stage-based COTS population model.

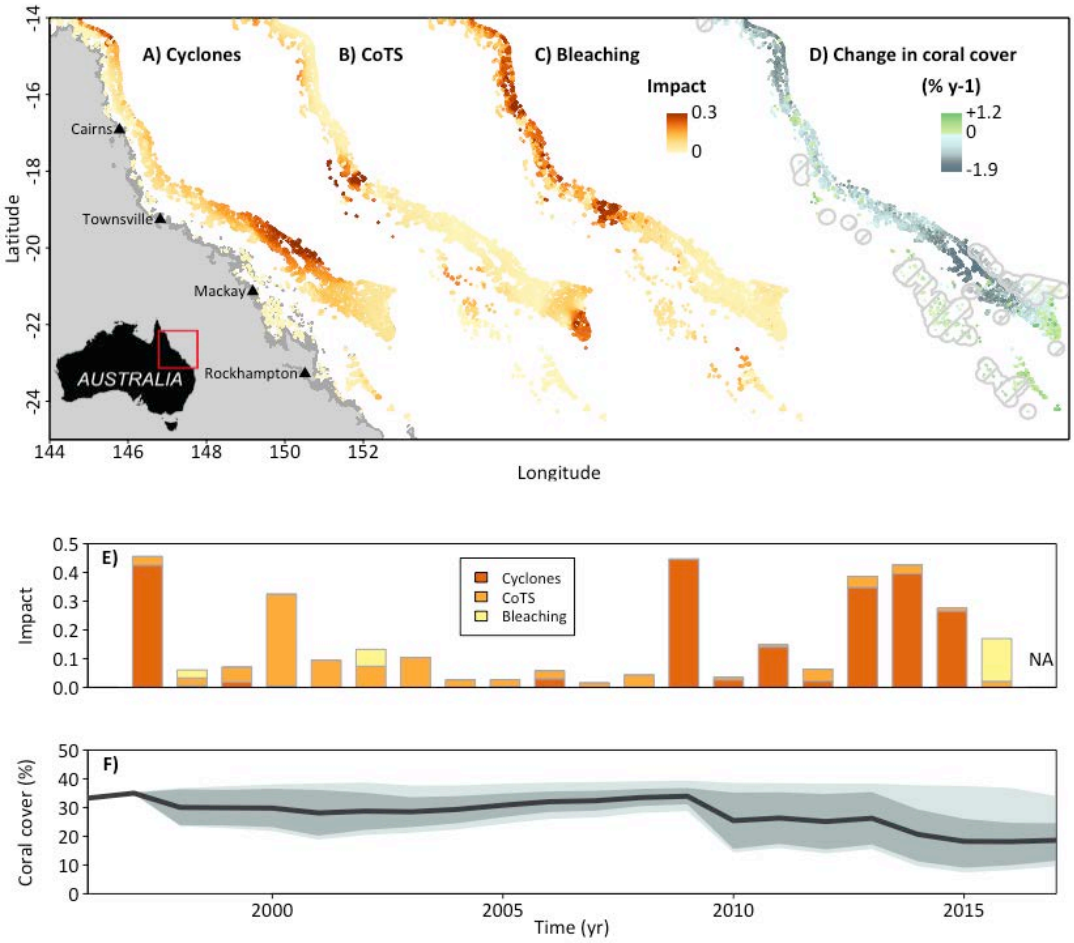

Figure 6.2 Results from the spatially explicit model of coral growth, disturbance and recovery from (Mellin et al. 2019a), depicting the average impact from A) Cyclones, B) COTS, C) Bleaching, and D) the mean percent change in coral between 1996-2017, E) yearly estimates of disturbance impact and F) median coral cover (+/- 50%, 90% confidence intervals). This model provides the framework upon which the COTS-Coral metacommunity model is constructed

6.3.2 COTS Population Model

To represent COTS demography, we developed a stage-based metapopulation model with a larval, two juvenile and an adult stage (Figure 6.3). Basic life history parameters include rates of density dependent mortality across age cohorts, density-dependent fertilization and feeding rates on corals. Stage-specific mortality rates and fertilization rates were modeled as a function of conspecific densities and resource availability within each 1x1km grid cell. Initial values for these parameters were based on estimates from the literature where possible, and otherwise

from expert opinion (Pratchett, unpublished data) (Table 6.1). Stage-specific COTS consumption rates, also drawn from the literature, enable the COTS population model to link with the coral growth model as an additional disturbance factor. Importantly all the initial parameters estimates discussed here are allowed to vary within the model framework to test the sensitivity of model predictions to changes in estimates used.

Table 6.1 Equations and sources for the population dynamics of COTS and Coral populations and vital rates for the demographic components of the COTS model where COTS abundances and coral cover are defined for the ith grid cell at the rth reef in year y.There are 4 **COTS life stages** in the model (A=Adults, J2 = Subadult; J1= Juveniles, L= Larval), which are defined by: $Pred_L$ = larval predation rate; $Surv_L$ = Larval survival as predicted by the logit chlorophyll model derived from Fabricius et al (2012); $CONN$ = average connectivity potential between reefs on the GBR; $Mort_{J1}$ = logistic density dependent mortality juvenile COTS; $Mort_{J2}$ = logistic density dependent mortality sub-adult (J2) COTS. $Mort_A$= Ratio dependent mortality for adult COTS (A); FvD = Von Bertnanffly growth curve for fertilisation by density; Fec = Ratio-dependent per capita fecundity for female COTS; Fec_{max} per capita fecundity without resource limitation; $CCRatio_1$ = ratio dependent thresholds onset of ratio-dependent fecundity and adult mortality; $CCRatio_2$ threshold below which COTS populations collapse; **Hard Coral Cover:** HC = Hard coral cover; r_s = intrinsic coral growth rate; α = strength of density dependence for sessile species; $\beta_j\ Disturb_{j,y}$ = Effect size and Estimate for jth disturbance (bleaching, cylones, disease, other); PF = combined exposure to flood plumes.

Name	**Equation**	**Source**
Stage Transition Rates		
$COTSL$	$N_{y,L_i} = N_{y,A} \times Fec \times FvD \times (1 - Pred_L) \times Surv_L$	NA
$COTSJ1$	$N_{y+1,J1_i} = \left(\sum_i^r N_{y,L_i} \times CONN_{ri,y}\right) \times (1 - Mort_{J1})$	
$COTSJ2$	$N_{y+1,J2_i} = N_{y,J1\ i} \times (1 - Mort_{J2})$	
$COTSA$	$N_{y+1,A_i} = N_{y,J2_i} \times (1 - Mort_A)$	
Coral Growth		
$Coral$	$log(HC_{y+1,i}) = r_{s,i} + (1 - \alpha_i)\ log(HC_y) + \sum_j \beta_j\ Disturb_{j,y} + \sum_j \beta_j\ Disturb_{j,y} \times PF_i$	(MacNeil et al. 2019, Mellin et al. 2019a)
Vital Rates		
FvD	$L_\infty\left(1 - e^{-K(N_{y,A})}\right);\ L_\infty = 0.8, K = 0.0007$	(Babcock et al. 1994, Rogers et al. 2017)
$Pred_L$	$N(\mu_P, \sigma_P);\ N(0.98, 0.01)$	(Scandol 1999)

$Surv_L$	$logit(Surv_L) = \beta_0 + \beta_1 log_2([Chl])$; $\beta_0 = [-0.4, 10], \beta_1 = 2.02$	(Fabricius et al. 2010, Wolfe et al. 2017)
$Mort_{J1}$	$\frac{L}{1 + e^{-k(N_{J1} - x_0)}}$; $L = 1$; $k \sim N(-2e^7,\ 0.5e^7)$; $x_0 \sim N(1e^{-7}, 0.2e^{-7})$	NA
$Mort_{J2}$	$\frac{L}{1 + e^{-k(N_{J1} - x_0)}}$; $L = 1$; $k \sim N(-7e^4,\ 2e^4)$; $x_0 \sim N(2.5e^{-5}, 0.5e^{-5})$	NA
$Mort_A$	$f\left(\frac{HC}{COTS_A}\right) = \begin{cases} 1, & for \frac{HC}{COTS_A} < CCRatio_2 \\ b \times \frac{HC}{COTS_A} + 1, & for\ CCRatio_2 < \frac{HC}{COTS_A} < CCRatio_1 \\ 0.1, & for \frac{HC}{COTS_A} \geq CCRatio_1 \end{cases}$	(Scandol 1999, Sweatman et al. 2008)
Fec	$f\left(\frac{HC}{COTS_A}\right) = \begin{cases} Fec_{max}, & for \frac{HC}{COTS_A} \geq CCRatio_1 \\ \left(b \times \frac{HC}{COTS_A} + 0.1\right) Fec_{\max}, & for \frac{HC}{COTS_A} < CCRatio_1 \end{cases}$	(Babcock et al. 2016b, Caballes et al. 2016)
Fec_{max}	$N(\mu_F, \sigma_F)$; $N(2e^7, 1e^7)$	(Babcock et al. 2016b)

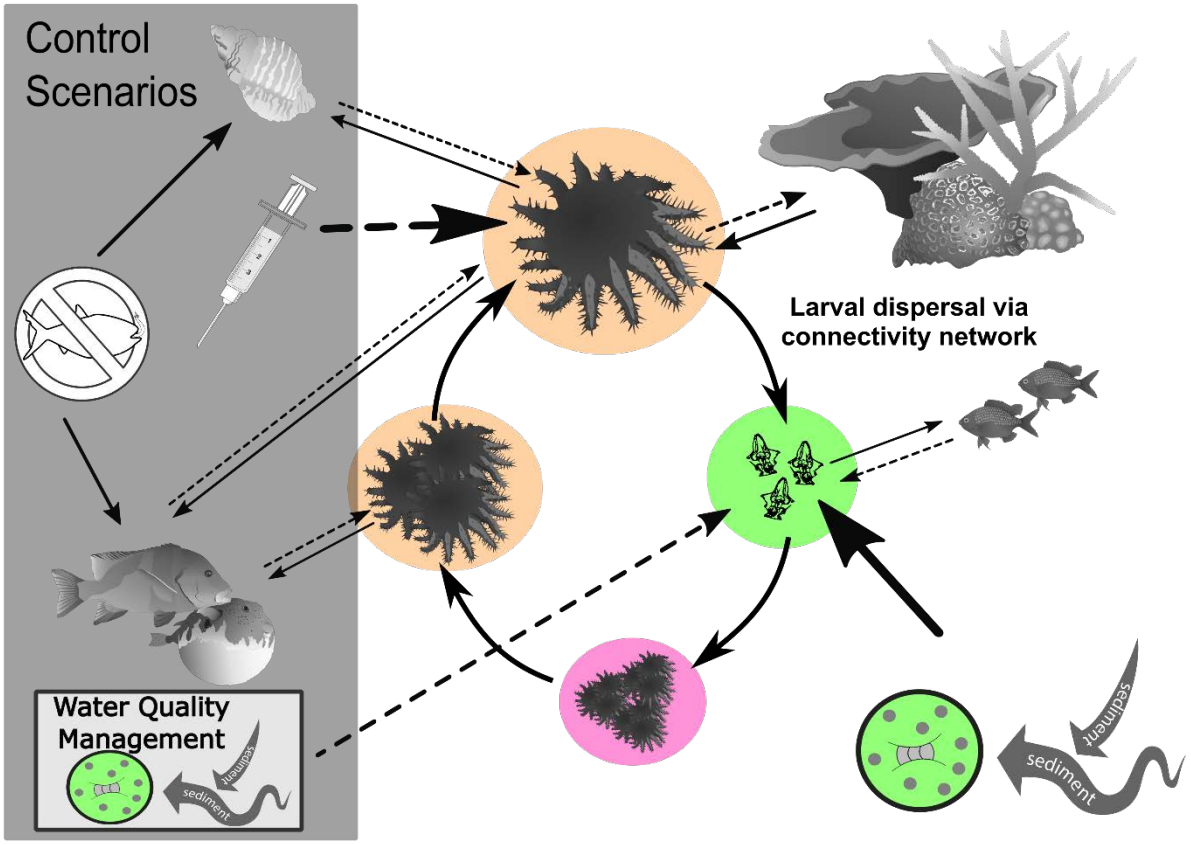

Figure 6.3. Conceptual diagram of the main factors involved in COTS outbreaks on the GBR and their relationship to various stages of the COTS life cycle. The white area represents the interactions currently included in the COTS-Coral metacommunity model, the shaded portion of the diagram represents potential management scenarios that could be incorporated into the modelling framework for projections. Coloured circles represent COTS food source for that life stage (green = phytoplankton/chlorophyll; pink = crustose coralline algae; coral = scleractinian corals). Solid lines represent a positive effect and dashed lines indicate a negative effect. Symbols are courtesy of the Integration and Application Network, University of Maryland Centre for Environmental Science (ian.umces.edu/symbols/).

Adult mortality and fecundity rates are assumed to be linearly dependent on the ratio of available coral prey for each adult COTS (Figure 6.4c,d). Coral cover-COTS ratio ($CCRatio$) was defined as % $Hard\ Coral\ Cover/COTS\ per\ manta\ tow$. Two thresholds were defined with respect to $CCRatio$, $CCRatio_1$ aims to capture the ratio at which coral cover is expected to decline as a result of consumption of COTS (20-40 % Hard Coral Cover/COTS per manta tow, depending on coral cover levels (Babcock et al. 2014)). At this threshold it is assumed that coral prey resources become scarce - increasing mortality, decreasing maternal nutrition and therefore reducing fecundity (Caballes et al. 2016). In the model, fecundity (mortality) is highest (lowest) at large values of $CCRatio$ and decreases (increases) linearly towards its minimum (maximum)(Figure 6.4). The maximum and minimum fecundity also use starting estimates from the literature (Babcock et al. 2016b). A second threshold $CCRatio_2$ was defined

to capture the recurring dramatic collapse of COTS populations observed in the AIMS LTMP data (Figure 6.1b), below which the mortality rate was set to 100% (Table 6.1). This threshold was determined using empirical observation data from the AIMS LTMP (Figure 6.4a,b). We used two approaches to identify initial values $CCRatio_1$ and $CCRatio_2$. Firstly, we fit a generalized additive mixed model (GAMM) to the proportional change in COTS populations (-1 to 1) in the year following a recorded COTS outbreak (> 0.22 individuals Manta Tow^{-1}) as a function of $CCRatio$, using cross shelf location as random factor (Figure 6.4a). Whilst this model did not explain a significant amount of variation (GAMM: R^2=0.03, p=0.11), it suggests a threshold for $CCRatio$ between 5-12 where COTS populations beginning to decline drastically. The second approach was to model change in COTS population size (in the following year) for populations exceeding severe outbreak threshold (> 1 individuals Manta Tow^{-1}) as a binary outcome in a generalized linear mixed model framework (increase in COTS density = 1; >50% decrease in COTS density = 0) to identify the $CCRatio$ at which increased mortality is triggered (Figure 6.4). Despite a high level of dispersion in the data, results declining $CCRatio$ is significantly related to COTS population crashes (GLMM; R^2= 0.11, p<0.01). Importantly, there is no recorded case of COTS population increase below a Coral-COTS ratio, $CCRatio$ of 4.6 (Figure 6.4b). From these results and the work of Babcock et al. (2014) we chose initial values of 5 for $CCRatio_2$ (threshold below which COTS populations

collapse) and 25 for $CCRatio_1$ (threshold below which COTS mortality and fecundity are negatively affected).

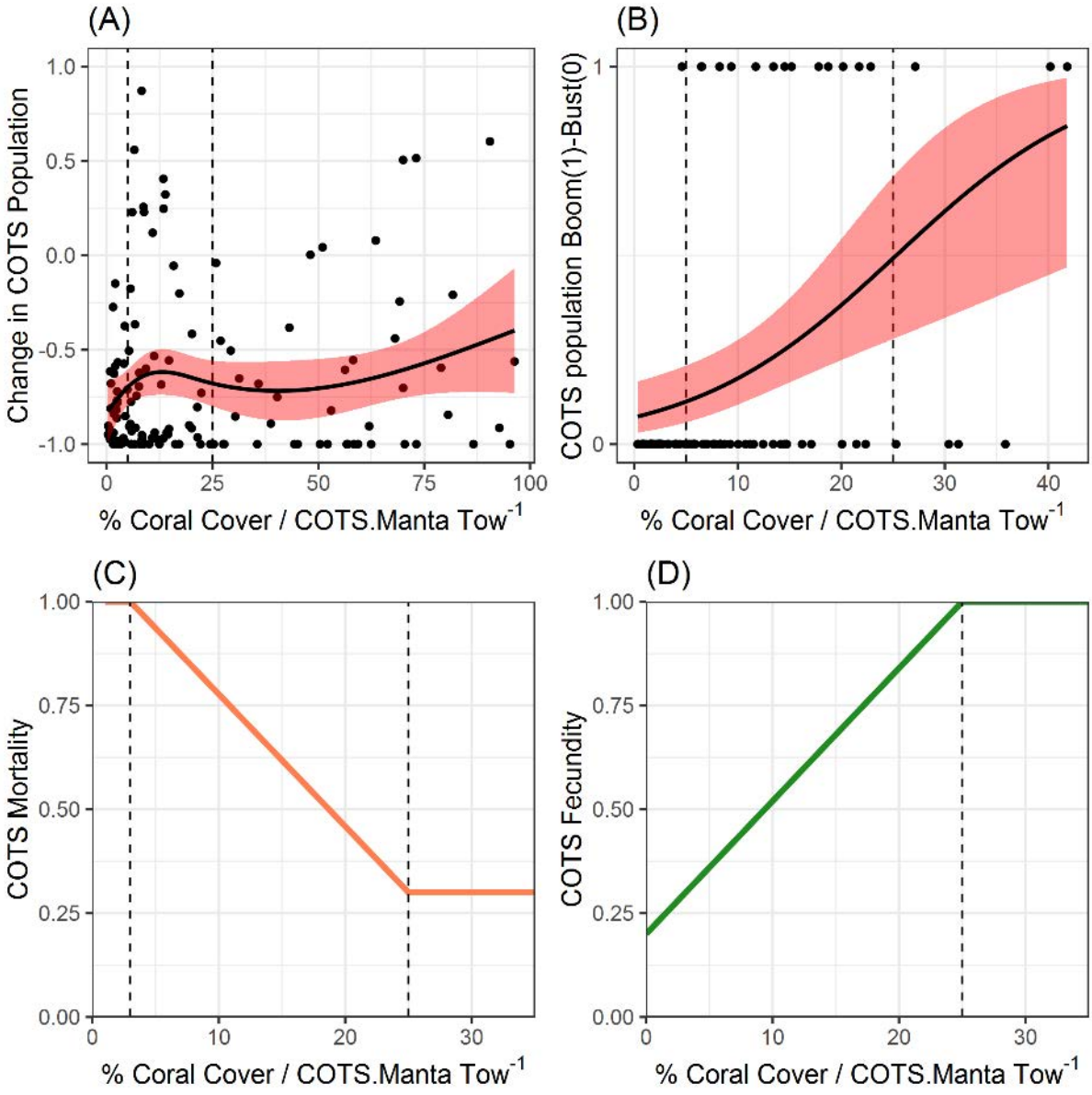

Figure 6.4 A) GAMM model for proportional COTS population declines following extreme COTS outbreak densities ; B) Binomial Relationship between Coral Cover-COTS ratio and the change to COTS population in the following survey year from AIMS LTMP data to provide initial estimates for ratio dependent thresholds used in the metacommunity model. C) Schematic of potential initial values for ratio-dependent thresholds for COTS mortality and D) Fecundity in relation to coral cover-COTS ratios.

We modeled juvenile and sub-adult COTS mortality as a function of COTS density (we chose not to use a ratio-dependent model for these life stages as juveniles feed on crustose coralline algae, while there is no data on sub-adult densities to estimate ratio-dependent thresholds)

within each 1km grid cell according to a standard logistic growth model. We initially parameterized these relationships on the basis of estimates of COTS densities at critical outbreak thresholds (De'ath 2003)(Table 6.2). Using these thresholds we estimated the number of juveniles and subadults present via an approximate estimate of COTS stable stage distribution generated using the R package 'popbio'(Stubben and Milligan 2007) and vital rates from Table 6.1.

Table 6.2 Estimated densities of different life stages of COTS at varying levels of Outbreaks to provide initial estimates for density dependent mortality curves. Adult densities are estimated using the calibration of De'ath (2003), *whilst earlier life stages are estimated from an approximate stable stage distribution.

COTS/Manta Tow	**Outbreak Status**	**Approx Adult Density (Adult ind km^{-2})**	***SubAdult Density (J2 ind km^{-2})**	***Juvenile Density (J1 ind km^{-2})**
0.01	No Outbreak	1000	6900	390000
0.1	Potential	3500	23600	1354000
0.22	Established	5100	33500	1923000
1	Severe	11100	71900	4122000

6.3.3 Larval Survival Model

To incorporate the well-established positive effects of prey availability on COTS larval survival (Fabricius et al. 2010, Uthicke et al. 2015b, Wolfe et al. 2015, Pratchett et al. 2017b), a logistic model of larval survival in relation to chlorophyll concentrations ([chl-a]) was developed based on the results from Fabricius et al. (2010). Other research has shown COTS ability to survive in oligotrophic conditions to be much higher than those estimated by this model (Wolfe et al. 2015, Pratchett et al. 2017b) and thus the intercept and slope term of this relationship were included as a model parameter for tuning. This provides the opportunity to

test the sensitivity of model predictions to this crucial relationship, within empirically supported bounds.

In order to model larval survival, [chl-a] was estimated for the period 1996-2017 using the 4x4km eReefs biogeochemical model for the GBR (CSIRO 2019). This model has produced [chl-a] estimates between 2010-2017 that we used to determine the reef-level relationship between [chl-a] and ENSO cycles. On the GBR, ENSO is commonly linked to rainfall, with strong La Niña events increasing rainfall and thus nutrient enrichment (Devlin et al. 2001, Lough 2001) and larval survival. Additionally, La Niña phases of the ENSO cycle are broadly linked to upwelling and phytoplankton blooms (Steinberg 2007) and thus using ENSO for hindcasting offers an opportunity to incorporate variation in [chl-a] from both rainfall and upwelling events. For each reef, a GAM was fit to determine the relationship between ENSO (using the September-November Nino 3.4 index (Rayner et al. 2003)) and [chl-a], and thus hindcast to 1996 using historical Niño 3.4 data (Table S 9.10)(Figure 6.5a,b). For each year of available eReefs data a matern variogram model (Matérn 1960, Rossi et al. 1992) was fit to determine the spatial autocorrelation in the model residuals, and a mean psill and range were calculated to determine the variogram model for La Niña, El Niño and neutral years. A total of 100 spatially correlated random replicate sets of chlorophyll predictions were then generated

for each year based on the ENSO estimate to provide sub-reef (1x1km grid cell) level variability and incorporate uncertainty in model estimates.

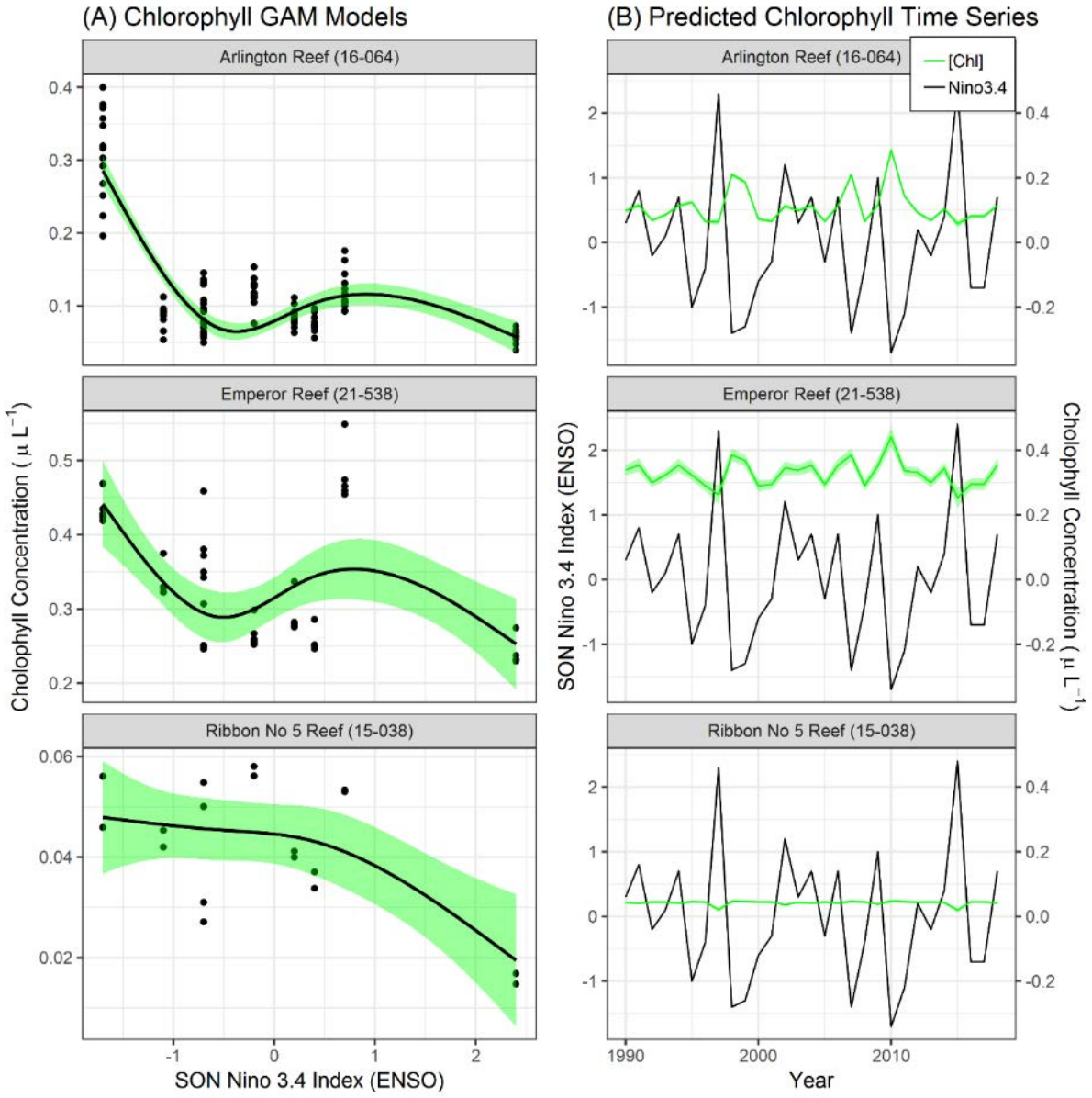

Figure 6.5 (A) GAM models fitting ENSO Nino 3.4 index to eReefs predicted chlorophyll concentrations for 3 reefs with variable background concentrations and (B) the predicted chlorophyll concentrations for the period 1990-2018 (Green) overlaying the Nino 3.4 index (black line).

6.3.4 Larval Connectivity Model

Estimates for larval connectivity between reefs on the GBR were obtained from Hock et al. (2017). These connectivity networks are constructed from 4 years of hydrodynamic modelled data and estimate the mean potential connectivity between all reefs on the GBR. Potential connectivity (expressed as a proportion) is a simplification of real-world processes which

essentially represents maximal physically possible advective transport among reefs as implied by the model (Hock et al. 2014). During the dispersal phase of our model, surviving larvae from each source reef were pooled at the reef level and then distributed among connected reefs using the strength of each connection averaged from the 4 years of modelled estimates. Larvae are then evenly distributed among the grid cells at the sink reef, and thus did not take into account the potential for larvae to be attracted to either prey or conspecific aggregations.

6.3.5 Model Validation and Sensitivity Analysis

Model predictions were calibrated using AIMS LTMP manta tow to generate a base case model that provided the best fit to the data. Reefs chosen for validation were surveyed at least 10 times providing reef wide estimates of coral cover and COTS densities (N=46). Predictions were then validated against reefs within the AIMS LTMP dataset that were not included in the 46 reefs used for calibration, yet included over 5 years of data (N=91). Using the initial parameter variables (Table 6.1), we used Latin Hypercube Sampling (McKay et al. 1978, Carnell 2009) to sample evenly across the parameter space, were starting values were varied by +/- 20%. For each parameter combination 100 simulated model runs were conducted to provide an estimate of the uncertainty of the stochastic (disturbance, chlorophyll concentrations and larval connectivity estimates), density and ratio-dependent elements of the model. Mean prediction error (MPE) for both COTS and Coral were estimated at each reef. Additionally for COTS, model accuracy (ACC) and kappa (KAP) statistics (Cohen 1960, Hossin and Sulaiman 2015) for predicting presence or absence of COTS outbreaks (OUT) (>0.22 COTS/Manta Tow) were calculated. ACC and KAP were also used to classify COTS across the four outbreak categories (Table 6.2).The parameter set which reduced prediction error and maximized prediction ACC an KAP (after ACC an KAP standardization to a 0,1 range) across all reefs was thus identified

as the base-case model (Eqn 1). For the base-case model, mean prediction error was aggregated for each latitudinal sector to give a spatial and overview of model performance.

$$V_m = \frac{(1 - MPE.HC_m) + (OUT.ACC_m) + (OUT.KAP_m) + (CL.ACC_m) + (CL.KAP_m)}{4} \quad [1]$$

Where $MPE.HC_m$ is the mean prediction error for hard coral estimates; $OUT.ACC_m$ and $OUT.KAP_m$ are the model accuracy and kappa statistic for the binomial classification of COTS outbreaks and $CL.ACC_m$ and $CL.KAP_m$ are the model accuracy and kappa statistic for multilevel classification of the four outbreak categories (Table 6.2). Additionally mean outbreak density was calculated for each latitudinal sector (Figure 6.1) as the mean COTS density (COTS/Manta Tow) for model estimates that exceeded the COTS outbreak threshold. This was compared to the values calculated for our validation reefs from the AIMS LTMP to investigate spatial variability in model performance in predicting COTS outbreak densities.

To identify the sensitivity of predictions to parameter estimates, 200 latin hypercube samples were drawn with each parameter varying within +/- 15% of the bounds identified by the base case model. These parameter values were then scaled and used as explanatory variables for our validation metric V_m (Eq. 1) using boosted regression trees (BRT) (Elith et al. 2008) to determine the most influential parameters and interactions between them for determining model accuracy (Norton 2015). Additionally, these scaled variables were also used to predict annual coral loss and COTS accuracy in multilevel classification (No COTS, No Outbreak = <0.11, Potential Outbreak = <0.22, Established Outbreak = <1, Severe Outbreak >1 COTS/Manta Tow) to investigate the variables most influential for driving COTS densities and coral loss in our model. All models were constructed using R v3.4.1 (R Development Core

Team 2017), with tools for sensitivity analyses provided by the 'lhs' (Carnell 2009) and 'dismo' (Hijmans et al. 2017) packages.

6.4 Results

The base-case model calibrated against the long-term training dataset (1995-2017) had a mean prediction error (MPE) of 7.19% for coral cover across the entire time series, and a MPE of 0.01 COTS/Manta Tow and mean prediction accuracy of 80.6% for COTS Outbreaks (V_m= 0.83). There was substantial spatial variation to the accuracy of model predictions (Table 6.3) most notably for COTS outbreaks. COTS densities were overestimated in both the Capricorn Bunker (CB) and Whitsunday (WH) sectors, with peak densities, particularly in the Townsville (TO) and Swains (SW) sectors, being underestimated.

6.4.1 Spatial Patterns in COTS Outbreaks

Outbreaks were initiated in 1996 in the "initiation box", peaking between 1997-1998. Outbreaks in northern regions of the GBR peaked at slightly lower densities than those predicted for secondary outbreaks in the Innisfail, Townsville and Swain regions, however these peak densities were much lower than observed in the monitoring data (Table 6.3). Patterns for individual calibration reefs generally followed peaks and troughs in COTS densities, although the model tended to overestimate COTS abundance during the ~10-15 year break between outbreak cycles (Figure 6.6). Importantly, the second outbreak cycle beginning around 2010 was accurately predicted by the model. In southern regions however, the model produced a multiple boom-and-bust dynamic, where COTS densities collapsed and increased

again multiple times throughout the period, which was not supported by the empirical observations.

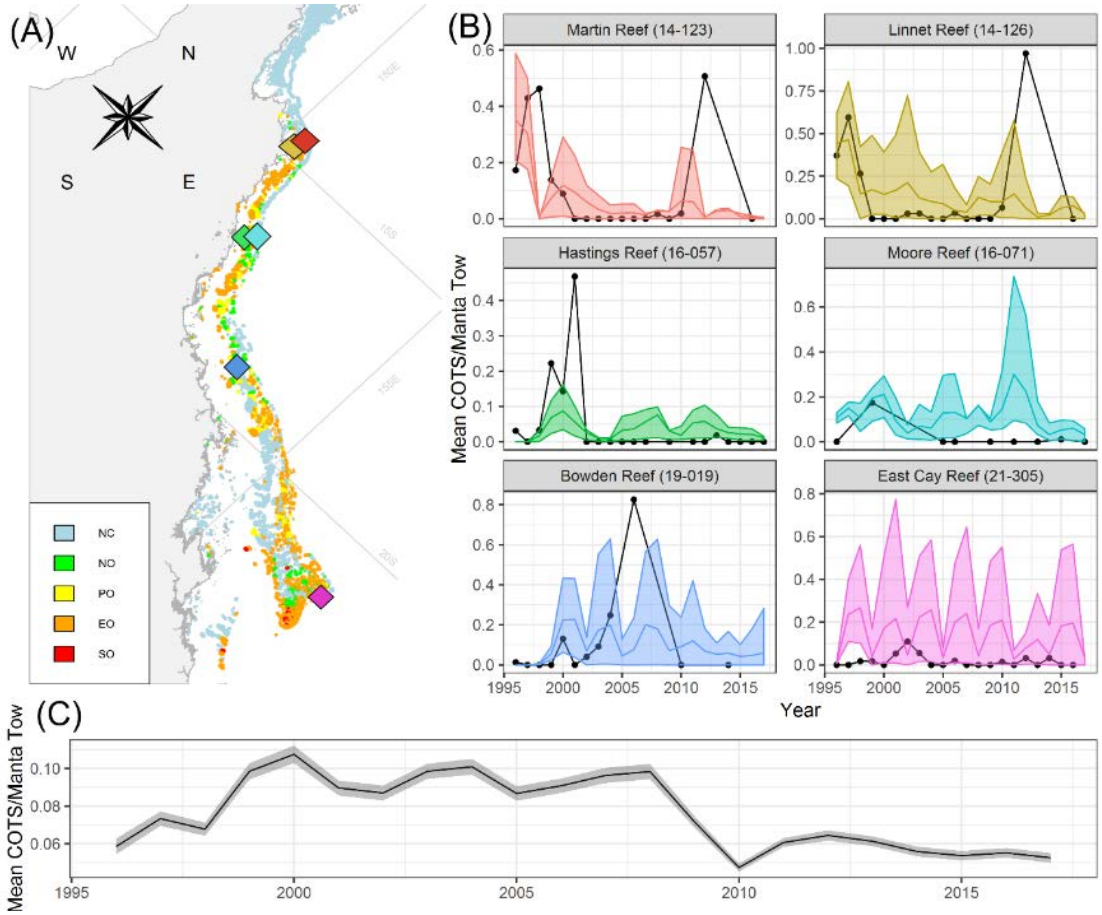

Figure 6.6 A) Predicted mean COTS abundance for each GBR reef with coloured diamonds matching reefs in B classified into outbreak categories in terms of COTS/Manta Tow; No COTS (NC) = 0; No Outbreak (NO) <0.11; Potential Outbreak (PO) <0.22; Established Outbreak (EO) < 1; Severe Outbreak (SO) > 1. B) Predicted mean (+/- 50% CI's) COTS/Manta Tow (Coloured ribbon) plotted against observation data (black dotted line) for six calibration reefs across the GBR. C) Predicted mean (+/- SE) COTS/Manta Tow, aggregated at the GBR level.

6.4.2 Spatial Patterns in Coral Cover

As coral cover was predominantly predicted from a previously calibrated model, the trajectories more closely match the empirical data (Figure 6.7b). Overall reefs in the Southern-Central (Pompeys and Whitsunday sectors) region of the GBR had the highest rates of coral decline, with the Northern region (Cairns and Cooktown/Lizard Island sectors) also

experiencing annual declines around 1% per year. However, some pockets of the GBR were predicted to experience annual increases in coral cover, particularly in the Capricorn Bunker and inner shelf Pompey sectors. Overall coral cover was predicted to decline 1.3% p.a. across the 22 years of the study.

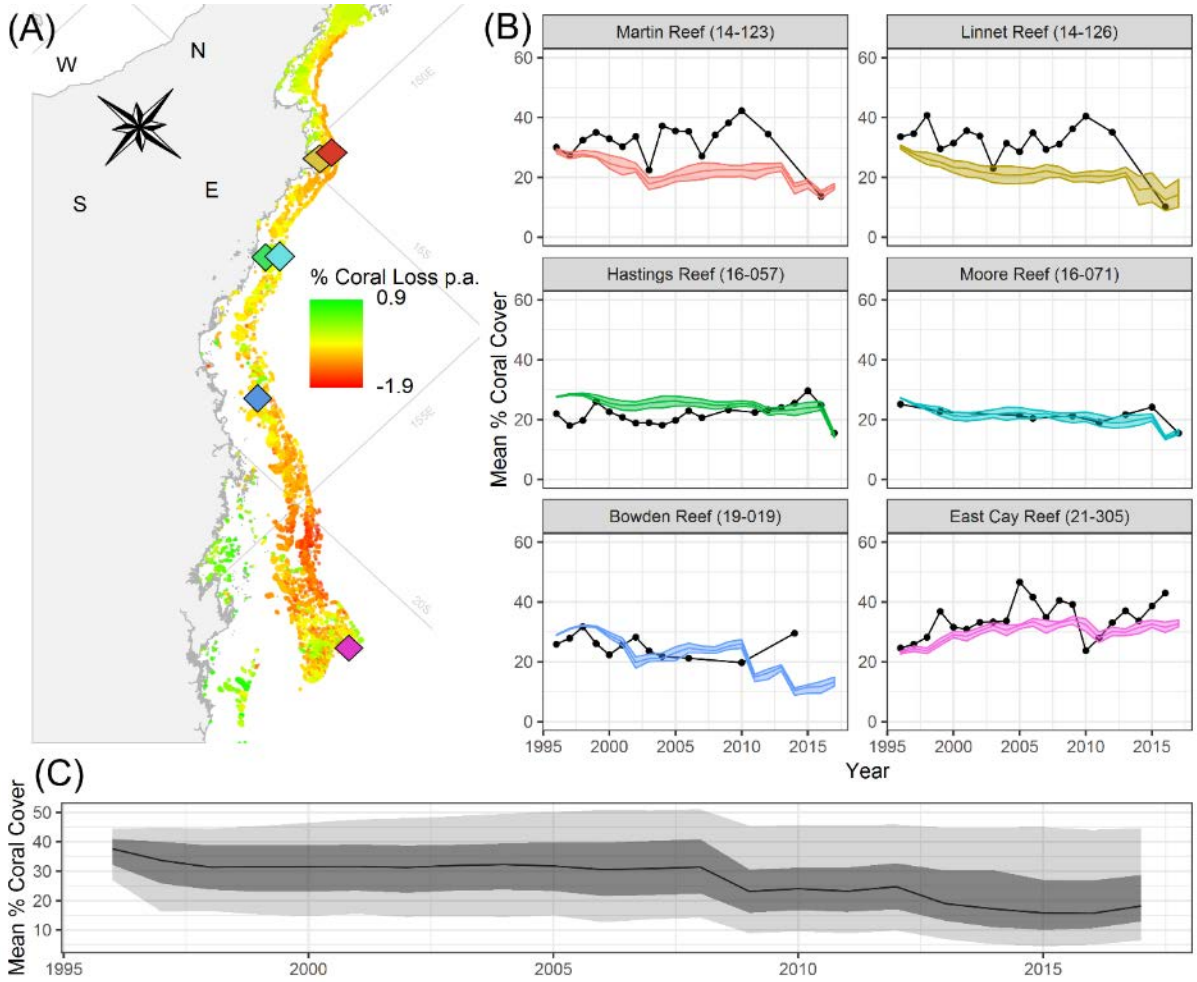

Figure 6.7 A) Predicted mean annual percent coral loss for each GBR reef with coloured diamonds matching reefs in B) Predicted mean (+/- 50% CI's) percent coral cover (Coloured ribbon) plotted against observation data (black dotted line) for six calibration reefs (colour coded diamonds). Predicted mean (+/- 50% and 95% CI's) percent coral cover, aggregated at the GBR level.

6.4.3 Model Validation

Predictions were validated against reefs within the AIMS LTMP dataset that were not included in the 46 reefs used for calibration, yet included over 5 years of data (N=91). For this independent dataset, our model captured the impact of multiple disturbances and subsequent

coral recovery (mean prediction error = 7.9%; R^2 = 0.14) performing similarly as for the calibration data (7.4% R^2=0.1). For COTS, whilst our model was able to recreate the general trajectories of COTS outbreaks (Figure 6.6), the accuracy of the model for predicting the presence or absence of an outbreak of COTS was insignificant for both calibration (Accuracy = 80.0%, Kappa = 0.193, $p > 0.05$) and validation (78.9%, Kappa = 0.014, $p > 0.05$) datasets (Table 6.3). Similarly, when classifying for the four outbreak levels model accuracy as insignificant for both calibration (Accuracy = 61.0%, Kappa = 0.176, $p > 0.05$) and validation (52%, Kappa = 0.04, $p > 0.05$) datasets. Additionally, for these models, the mean COTS outbreak density was overestimated in the Whitsundays and Capricorn Bunker sectors whilst underestimated for Swain, Townsville, Pompeys and Innisfail sectors, indicating a tradeoff between presence/absence accuracy and matching peaks in COTS outbreak densities within the model. Importantly, accuracy for predicting presence/absence of COTS was only marginally better than chance alone, indicating a general tendency to estimate low levels of COTS when none were observed in the data.

Table 6.3 Validation statistics for best-fit model parameters across latitudinal sectors of the GBR(Figure 6.1a PC = Prince Charlotte Bay; CL = Cooktown/Lizard Island; CA = Cairns; IN = Innisfail; TO = Townsville; CU = Cape Upstart; WH = Whitsundays; PO = Pompeys; SW = Swains; CB = Capricorn Bunker) where MPE = mean prediction error, ACC = model accuracy, KAP = Kappa and Outbreak Density = model predicted mean COTS/Manta tow when density exceeds 0.22 COTS/Manta Tow and Δ Outbreak Density is the % difference between model predicted outbreak density and AIMS LTMP Manta Tow observation.

Sector	MPE Hard Coral (%)	MPE COTS (COTS/MT)	Acc COTS Presence	Acc COTS Outbreak	Kap COTS Outbreak	Outbreak Density	Δ Outbreak Density
PC	2.81	0	0.36	0.82	0	NA	-100%
CL	7.60	0.066	0.69	0.91	0.51	0.50	2%
CA	2.52	0.010	0.80	0.98	0	0.46	35%
IN	4.29	0.057	0.29	0.85	0.17	0.53	-80%
TO	3.94	0.19	0.61	0.58	-0.074	0.65	-80%
CU	4.79	0.061	0.43	0.78	-0.12	0.67	46%
WH	6.94	0.049	0.78	0.92	-0.04	0.81	113%
PO	7.64	0.068	0.32	0.82	-0.10	0.67	-78%
SW	4.81	0.16	0.55	0.55	0.21	0.70	-92%
CB	7.29	0.15	0.82	0.76	0.18	0.64	94%
Overall	7.20	0.01	0.627	0.806	0.219	0.63	-81%

6.4.4 Sensitivity Analysis

Our sensitivity analysis (Figure 6.8) using boosted regression trees (BRT) revealed that overall model performance was most sensitive to variation in the constant for larval predation rate (BRT relative importance; $Pred_{Larv}$ = 46.7%), followed by the two parameters controlling the strength of density-dependent mortality for COTS J1 life stage ($MortJ1_{k}$ = 21.5%, $MortJ1_{k0}$=17.5%). The coral cover-COTS ratio below which COTS populations crashed was less influential in overall prediction accuracy ($CCRatio_{2}$ = 3.0%), alongside the maximum rate of fertilization of COTS larvae ($Fert_{Linf}$=2.0%) and maximum per capita fecundity fecundity (Fec_{max}=1.6%). Coral cover prediction error was most sensitive to larval predation rate ($Pred_{Larv}$ = 32.7%) and maximum coral consumption rate ($Cons_{max}$ = 22.6%). COTS multilevel

classification accuracy was most sensitive to early life stage parameters ($MortJ1_k$ = 44.8%; $MortJ1_{x0}$ = 34.6%; $Pred_{Larv}$ = 16.3%).

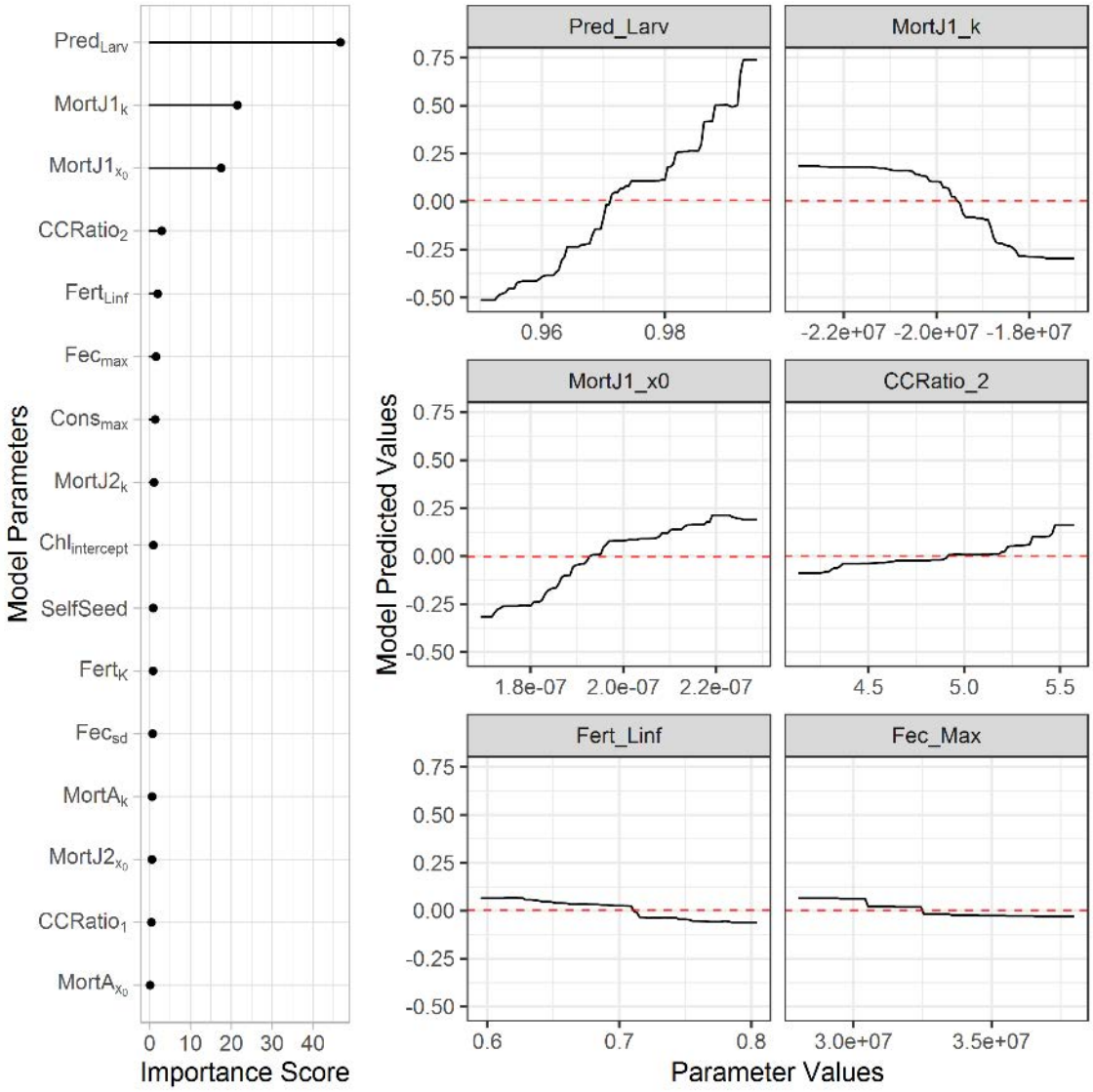

Figure 6.8 Relative importance and partial dependency of COTS population model parameters in improving overall accuracy based on the combined V_m validation metric where $Pred_{Larv}$ = larval predation rate; Mort = density dependent mortality parameters (A=Adults, J2 = Subadult; J1= Juveniles), CCRatio = ratio dependent thresholds for (1) onset of effect and (2) collapse of COTS populations; $Fert_{Linf}$ = max fertilisations rate; $Fert_k$ = rate parameter for fertilisation; Fec_{max} maximum fecundity per female COTS; Fec_{sd} = standard deviation for fecundity; $Chl_{intercept}$ = intercept term for the chlorophyll model, used to adjust larval survival; SelfSeed = Scaling parameter to alter the proportion of COTS larvae settling at home reef.

6.5 Discussion

Destructive outbreaks of COTS have been responsible for a significant portion of the loss of coral cover of the last 35 years and have thus been the focus of much research and management action (De'ath et al. 2012, Pratchett et al. 2017a, Mellin et al. 2019a). This research often

focuses on the hypothesized causes of outbreaks (Brodie et al. 2005, Wooldridge and Brodie 2015), control technologies (Rivera-Posada et al. 2014, Uthicke et al. 2018) or spatial patterns in outbreaks (Vanhatalo et al. 2017, Mathews et al, in prep). Moreover, previous modelling studies have generated small scale population models (Morello et al. 2014, Chen et al. 2017), larval connectivity networks (Hock et al. 2014), simulated hypothetical reef networks (Condie et al. 2018) or aimed to refine our knowledge of COTS life history characteristics (Rogers et al. 2017). Our work builds on this vast foundation of knowledge to provide a framework for spatially and temporally explicit predictions of Coral Cover and COTS abundances and fit them to the extensive observational data that exists for the GBR (Sweatman et al. 2008), whilst also accounting for the increasing cumulative disturbance in this region (Matthews et al. 2019).

Model predictions were generally able to match the timing of peaks in outbreak densities and provided reasonable predictions of the presence or absence of COTS outbreaks. Importantly, following the initiation of COTS populations in 1996, the model was able to produce peak densities between 1996-1998 for northern reefs in the Cooktown/Lizard Island and Cairns sectors (Figure 6.6) whilst those further south in the Innisfail and Townsville sectors were predicted to experience peak densities between 1999-2001, similar to patterns in the observational data (Figure 6.1, Figure 6.7). This shows that, whilst COTS densities during an outbreak are difficult to predict accurately, our model captured the spatio-temporal patterns of outbreaks as described by other modelling studies (Vanhatalo et al. 2017). In our model, these spatio-temporal patterns are driven primarily by the spatial and temporal variation in chlorophyll concentrations, larval connectivity and prey availability estimates. Our results indicate the utility of these modelled estimates and provide further evidence in support of larval nutrition (Birkeland 1982, Brodie et al. 2005) and larval connectivity (Hock et al. 2014, Wooldridge and Brodie 2015) , at least for explaining secondary outbreaks.

Some limitations on model performance surround the ability to recreate the extreme increases in COTS densities, most notably recorded in reefs in the Townsville and southern Swain regions. Using our best-fit model parameters, predictions of mean outbreak density in these regions were underestimated by 80% and 92% respectively (Table 6.3). Whilst higher densities

were predicted by some model configurations (results not shown), this generally led to overestimating densities in other regions and reducing overall model fit. Additionally, multiple boom-bust cycles were predicted on some Southern reefs that were not supported by empirical data. This is partly to ratio dependent thresholds in COTS density that promote population declines. This could be countered by forcing the model to only take into account prey-availability but would limit the model's ability to capture population decline when coral resources remain. Previous modelling attempts for COTS have run into similar issues in recreating peak densities, requiring for example larval input to be artificially introduced into the model to create the second wave of COTS outbreaks beginning 2010-2012 (Morello et al. 2014). We estimated a time series for chlorophyll-a using the consistent link between ENSO and chlorophyll-a to drive COTS outbreaks and our model was able to reproduce these peaks without any artificial data manipulation. This is a novel and useful approach to predicting for missing years in chlorophyll-a data however more development is required to accurately capture dramatic peaks in COTS densities.

A number of alterations to the model structure could potentially improve model fit with regards to spatial variability in peak COTS outbreak densities. For example, allowing the threshold that triggers outbreak collapse to vary for each latitudinal sector and cross shelf location combination as estimated by the empirical data, could provide a mechanism for promoting these more severe densities in specific areas. This approach, whilst not allowing these regional differences to emerge intrinsically from the model, may significantly improve model fit. Allowing these regional differences in mean COTS outbreak density would act as a proxy for calculating spatially explicit carrying capacities that could account for some variation not captured by our current approach. Primarily, as COTS exhibit significant feeding preference for fast growing corals, especially table and branching *Acropora spp.*(Pratchett 2007), reefs with naturally higher proportions of these species should exhibit higher outbreak densities and thus higher carrying capacities. Increased COTS densities can be explained by both increased food supply supporting more adult COTS and increased maternal nutrition leading to significantly higher rates of larval success (Caballes et al. 2016, 2017a). There is also potential

to incorporate estimates of coral benthic community type (Mellin et al. 2019a) to help define peak outbreak densities, by allowing reefs predicted to be *Acropora* dominated to reach higher thresholds. Additionally, incorporating a "no settlement" or limited settlement period following a collapse, to simulate the attraction of larvae to other nearby reefs with dense adult populations (Cowan et al. 2016) may help capture periods of low density populations. This would lower the influence of parameters that control rapid expansion of COTS and promote more dramatic peaks, without overestimating COTS abundance during the non-outbreak cycle.

Whilst our model incorporates contemporary GBR-wide estimates of COTS larval connectivity, better integration of inter-annual variability in connectivity pathways provides an opportunity to improve model estimates. Larval connectivity pathways are hypothesized to be pivotal in determining COTS spatial distribution during waves of secondary outbreaks (Hock et al. 2014) and, together with primary productivity, inter-annual variability in connectivity has been linked to the initiation of primary outbreaks (Wooldridge and Brodie 2015). Incorporating more interannual variability in connectivity estimates will likely increase the model performance in capturing peak densities at outbreaking reefs since, due to COTS immense fecundity (Babcock et al. 2016b), any fractional increases in the proportion of larvae arriving at a reef may dramatically increase adult densities. The distribution of arriving larvae in this study was uniform across a reef and did not allow for the attraction of larvae to either coral prey or conspecifics. This would potentially tend to underestimate population establishment through fertilization success and local recruitment and may help to explain the lack of peak densities predicted for some reefs/sectors. Importantly, the connectivity estimates used in this study have received warranted scrutiny in their ability to accurately predict connectivity pathways primarily due to the relatively coarse spatial resolution (4km) (Bode et al. 2018, Mumby et al. 2018). Further development of the hydrodynamic models of the GBR to incorporate unstructured meshes and finer resolutions (Thomas et al. 2014) should increase the accuracy of these estimates and ultimately the predictions of regional scale ecosystem models. Additionally, recent important advances in satellite imaging have rapidly developed the understanding of potential coral habitat along the GBR (Roelfsema et al. 2018), and

incorporating these underlying habitat maps are essential for the refinement of both connectivity models and metacommunity models for the GBR.

Our model makes use of a machine learning approach to sensitivity analyses to identify important parameters when optimizing overall model accuracy, coral cover estimates or COTS outbreak classification (Norton 2015). This approach highlighted that predictions were particularly sensitive to parameters controlling early life stages such as larval predation rate and density dependent juvenile mortality. Due to the demographic traits of the species (Babcock et al. 2016b), such sensitivity was anticipated, and indeed predatory and density related mortality rates of early life stages represent bottlenecks in COTS population dynamics yet have remained key gaps in the understanding of COTS outbreaks (Pratchett et al. 2017a). Whilst some recent work has highlighted potential predators of COTS larvae (Cowan et al. 2016, 2017b, 2017a) and investigated juvenile predation rates (Wilmes et al. 2019), generating spatially and temporally explicit predictions of predator abundance or a suitable proxy seems beyond the scope of contemporary research. Potentially incorporating the effects of marine park zoning could account for some predatory effect on COTS larvae, however most identified predators of larvae and juveniles are not targeted by fishing activities (Cowan et al. 2017a) although they could indirectly impacted by fishing (e.g. habitat loss due to anchor damage). Moreover, given the links between outbreak probability and zoning are poorly understood (Sweatman 2008, Vanhatalo et al. 2017), a zoning parameter seems unlikely to drastically improve model performance. Alongside zoning, incorporating minor spatial and temporal stochasticity to the early life stage parameters provides clear improvements to the current framework.

Our model provides the first framework for predicting coral cover and COTS densities in a spatially and temporally explicit manner, for reef locations across the GBR. Whilst improvements are required to fine-tune parameters, this framework provides a solid basis for further development, with scope to incorporate proposed management interventions and projections towards the next outbreak cycle. During the course of the most recent outbreak on the GBR there have been vast improvements to both control technologies and strategies

(Westcott et al. 2016), with a number of emerging technologies being investigated to help with the early detection of outbreaks (Doyle et al. 2017, Uthicke et al. 2018), use of pheromones for COTS aggregation and/or dispersion (Hall et al. 2017a, 2017b) and remote autonomous surveillance (Llewellyn and Bainbridge 2015). If deployed effectively (in time and space), some combination of these technologies may prove to be pivotal to reducing the impact of the next wave of COTS outbreaks. Incorporating a range of intervention strategies into our modelling framework would provide an avenue to empirically assess the probability of curtailing the next outbreak cycle and/or protecting high priority areas of the GBR to bolster the resilience GBR (GBRMPA 2017, Hock et al. 2017). Additionally, developing probabilistic models for disturbance events based on disturbance history could provide an avenue for running these models into the future to determine the effect of COTS outbreaks as disturbance severity and frequency are predicted to increase (Hughes et al. 2018a, Great Barrier Reef Marine Park Authority 2019). To achieve this goal, future projections of chlorophyll concentrations and connectivity patterns could be projected forward based on historical data, climate change projections, ENSO cycles and a variety of water quality management scenarios.

This study aimed to provide the first spatially and temporally explicit COTS-Coral metacommunity model for the GBR, at a 1x1km resolution. Whilst successfully recreating the trajectories of coral cover and COTS outbreaks, it is currently not able to capture some of the spatial variability with regards to peak outbreak densities. It is important to note that fine-scale models such as these have low generality and thus forecasting skill, and are thus designed to simulate current conditions and management strategies and limited to near future forecasting (i.e. the next COTS outbreak cycle). Furthermore, in its current configuration, the model tends towards overestimating COTS abundances during low density years and does not differentiate between fast and slow growing corals. This study highlights critical knowledge gaps to set priorities for ongoing biological research (e.g. predation rates, natural mortality rates) and also key areas for improvement to this model framework, in order to better capture the spatial and temporal variability in COTS densities. The major improvements required include improving estimates of inter-annual variability in larval connectivity estimates and incorporating sector-

and shelf-level variation in the density dependent thresholds used to promote crashes of COTS populations in the model. Whilst improvements need to be made, this modelling framework is the first of its kind for the GBR and provides a platform upon which a variety of COTS management scenarios could be simulated. Further developing this framework will provide important guidance for the prioritization of reefs for COTS control as well as the combination of management strategies most likely to help protect coral cover in the next wave of COTS outbreaks.

7 General Discussion

7.1 Cumulative disturbances and abiotic characterization of the GBR

The Great Barrier Reef (GBR) has been subject to protracted and intensifying chronic and acute disturbances for several decades, resulting in sustained declines in coral cover (De'ath et al. 2012, Mellin et al. 2019a - Chapter 5). Despite a long history of proactive, expansive and adaptive management (GBRMPA 2004, McCook et al. 2010b), the GBR faces an uncertain future in the context of intensifying and cumulative disturbances (Knutson et al. 2010, Maynard et al. 2015, Uthicke et al. 2016, Hughes et al. 2017b). In recent years, researchers have begun to focus on quantifying the impact and interactions between multiple disturbances in order to try to address this uncertainty (Osborne et al. 2011, Ortiz et al. 2018, MacNeil et al. 2019). For example MacNeil et al (2019 – Appendix 9.7) determined the negative effect size of individual disturbances (cyclones, bleaching, COTS, disease) on coral growth and disturbance recovery and how these interacted with poor water quality. This research showed that while poor water quality may offer some resistance to bleaching, it reduces the recovery rate and makes reefs more prone to oubtreaks of COTS and coral disease. Recovery rates on the GBR have also been reduced as a result of the cumulative effect of chronic stressors (warming, water quality) and acute disturbance events (Ortiz et al, 2018). These studies are however limited in their spatial scope, focusing on reefs for which extensive time series ecological data exists (Sweatman et al. 2008). In order to understand the effects of multiple disturbances on the GBR, datasets that catalogue the disturbance history and abiotic context for every reef (Matthews et al. 2019 -

Chapter 2) are required as a platform for regional scale simulation modelling to both recreate the history (Mellin et al. 2019a - Chapters 5,6) and predict the uncertain futures for the GBR.

On the GBR, there are extensive data repositories for observational and modelled ecological, biogeochemical and hydrodynamic data (e.g eAtlas: https://eatlas.org.au/, eReefs: https://research.csiro.au/ereefs/, Eye on the Reef: http://www.gbrmpa.gov.au/eye-on-the-reef/, Coral Reef Watch: https://coralreefwatch.noaa.gov/satellite/product_overview.php). Groundbreaking studies and monitoring programs have provided large scale estimates for the most common disturbances to the GBR such as cyclones (Puotinen et al. 2016) thermal stress (Heron et al. 2016, Liu et al. 2017), bleaching (Berkelmans et al. 2004, Hughes et al. 2018b) and outbreaks of COTS (Sweatman et al. 2008), as well as characterizing environmental conditions (Huang et al. 2013). These data however have remained siloed and have yet to be compiled and distributed on a standardized grid. Chapter 2 of this thesis collated these data as a platform for regional-scale modelling of the GBR (Chapters 4-6). The aim of this endeavour was not only to collate the data necessary for the modelling of later chapters, but for the use of the wider research community to promote collaboration and reduce the duplication of effort of working groups working on related goals. The dataset has been used as the disturbance history and abiotic context in studies determining the coral growth and recovery rates for GBR reefs (MacNeil et al. 2019), the spatial resilience of the GBR (Mellin et al. 2019a - Chapter 5), proposing adaptive monitoring networks for the GBR (Thilan et al. 2019), and also as elements of the Reef 2050 Integrated Monitoring and Reporting Program (GBRMPA and Queensland Government 2015).

Management on the GBR has become increasingly focused upon developing monitoring, reporting and modelling tools that that make use of the extensive empirical and modelled data that exists for the GBR (GBRMPA 2017, GBMRPA and Queensland Government 2018). It is important to ensure that these data do not become divided among research institutes and management agencies, but are easily transferred and integrated into spatial and analytical databases available to management agencies and researchers alike. Chapter 2 works towards this goal by collating data from multiple researchers, government agencies and existing

databases and providing data on a standard grid. However, in order to realize the goals of integrated monitoring and reporting programs, the production of these datasets should be partially automated to ensure estimates are up to date and does not rely on individual researchers processing data and providing it to a central organisation. For example, production of the COTS disturbance layers and Degree Heating Week data of Chapter 2 could be easily integrated into a larger reporting program as they rely on readily available data (Sweatman et al. 2008, Liu et al. 2017) and relatively simple R scripts for processing. While generating cyclonic wave estimates (Puotinen et al. 2016) and bleaching severity indices (Berkelmans et al. 2004, Hughes et al. 2017b) require more intensive modelling and field work respectively, it is important that these datasets are made widely available and incorporated into automated systems where possible. The production of standardized, centralized and freely available datasets is integral to reducing the duplication of effort, enhancing the productivity of, and collaboration between the research and management communities, and ensuring that research is conducted in a reproducible and consistent manner. Working towards these goals should be a key focus for management and researchers on the GBR in the coming years.

7.2 Adaptive management tools for data synthesis, analysis and visualisation

Of the major causes of coral loss on the GBR, outbreaks of COTS are the most amenable to direct intervention (De'ath et al. 2012, Westcott and Fletcher 2018) and have thus, been the focus of one the most extensive control programs in marine ecosystems (GBRMPA 2018a, Pratchett et al. 2018). The Great Barrier Reef Marine Park Authority (GBRMPA) coordinates the COTS Control Program which has been operating teams of divers on two vessels since 2012, with that effort increasing threefold as of November 2018. Aside from culling adult COTS, this program contributes extensive data from extensive manta tow surveys, Reef Health Impact Surveys (RHIS) and culling data across the GBR (GBRMPA 2018a). The Great Barrier Reef Marine Park Authority (GBRMPA) collects COTS and coral data through the joint Field Management Program (FMP) - Queensland Parks and Wildlife Services (QPWS) COTS

Response Program which has collected extensive manta tow (Bass and Miller 1996) and RHIS data (Beeden et al. 2014) since 2011, and the Eye on the Reef (EoTR) program which collects RHIS data through numerous tourism and local stakeholder groups. Overall GBRMPA collects data from over 10,000 individual surveys annually across the different programs (Chapter 3). While systems exist for the storage and maintenance of such data, there has yet been an attempt to synthesise all the available COTS observation data to provide a visualisation and analytical platform to aid in the adaptive management of COTS on the GBR. Importantly, the development of such analytical tools have been identified by GBRMPA as key priorities in the development of the planned Reef 2050 Integrated Monitoring and Reporting Program (Hedge et al. 2017, GBMRPA and Queensland Government 2018)

Advances in newly emerging BI software (e.g Microsoft Power BI) (Larson and Chang 2016) provide an opportunity for conservation interventions to leverage this innovation and aid in the implementation of adaptive management strategies. Chapter 3 of this thesis utilised the extensive ecological data collected by the GBRMPA and its partners to build an interactive visualisation and analytics platform for COTS, as the agency moves towards developing integrated monitoring and reporting tools (GBMRPA and Queensland Government 2018). The COTS Dashboard specifically aimed to address key elements of the adaptive management cycle by providing visualisations to (1) assess the extent and severity of outbreaks across the GBR; (2) track the implementation of management actions; (3) monitor and evaluate the progress made towards achieving ecological goals of the program and (4) provide engaging visualisation and flexible data summaries as tools for stakeholder engagement. Importantly, the Power BI platform is highly flexible, meaning that desired changes to the interface design, analysis or visual representation can be made rapidly, promoting the adaptive management ethos (Schreiber et al. 2004, Dobbs et al. 2011). Furthermore as the Dashboard was developed using Microsoft's Power BI, it does not require expert computer programming skills for further development and there is reduced risk that the software will stop being supported, which are common concerns with many decision support tools (Pınarbaşı et al. 2017). Indeed, tools such as the COTS Dashboard, characterized here as Conservation Intelligence (CI) tools should be

considered as important components to conservation interventions, particularly in date rich environments such as the GBR.

In the specific context of COTS outbreaks on the GBR, the COTS Dashboard is the first tool to synthesise the available observation data for COTS allowing these multiple disparate streams of data to be interrogated simultaneously. This is an important first step in understanding the complex spatial and temporal patterns of COTS data. Importantly, the flexible nature of the platform and interoperability with more advanced statistical platforms such as R and Python provides scope to incorporate more complex modelling and prediction into the platform (see Chapters 4-6). Moreover, this research provides an important proof-of-concept of the utility of such tools as the GBRMPA and conservation organisations more broadly look toward developing integrated monitoring and reporting platforms for data driven adaptive management (Stephenson et al. 2015, Weatherdon et al. 2017, GBMRPA and Queensland Government 2018).

7.3 Competing causes of crown-of-thorns starfish outbreaks on the GBR

COTS have been one of the most studied coral reef organisms, and there is a long history of research aiming to identify the underlying causes of, and contributors to, COTS outbreaks, yet several key knowledge gaps persist (Endean 1969, Birkeland 1982, Pratchett et al. 2017a). This research has focused on four primary areas: (1) identifying the life history characteristics of COTS that make them susceptible to boom-bust outbreak dynamics (Vine 1973, Uthicke et al. 2009, Babcock et al. 2016b); (2) the anthropogenic influence of the removal of predatory regulation of COTS populations via over-harvesting of natural predators (Endean 1969, Sweatman 2008, Cowan et al. 2017a); (3) the enhanced larval survival as a result of terrestrial runoff and elevated nutrient levels into the GBR lagoon (Birkeland 1982, Brodie et al. 2005); and (4) the role of hydrodynamics in retention versus dispersal of COTS larvae at the scale of individual reefs (Dight et al. 1990a, 1990b, Hock et al. 2014). While research has been relatively thorough for each of these lines of enquiry (Pratchett et al. 2017a), it has become

increasingly apparent that these factors act interactively (Wooldridge and Brodie 2015, Babcock et al. 2016a), and that single-factor hypotheses cannot explain the complex spatial and temporal patterns of COTS outbreaks.

While some recent research has compared these complementary hypotheses from a theoretical perspective (Babcock et al. 2016a), there has yet been an attempt to use the extensive observation data available (Sweatman et al. 2008, Chapter 3) to identify the most important variables for predicting COTS spatial distribution. Chapter 4 of this thesis created a species distribution model (SDM) for COTS presence, prevalence and outbreaks using an extensive dataset of environmental variables (Matthews et al. 2019 - Chapter 2) and COTS observation data (Chapter 3) in an ensemble framework comprising boosted regression trees (BRT) and generalized additive mixed models (GAMM). This model confirmed the importance of water quality indicators (e.g. chlorophyll concentrations, flood plume exposure) as well as suggesting the importance of temperature gradients in predicting patterns of COTS presence (Lamare et al. 2014, Hardy et al. 2014, Uthicke et al. 2015b). In contrast, our results suggested that sustained larval supply from reefs with COTS was required to establish more severe and/or prevalent outbreaks. Interestingly, these results showed no strong influence of no-take fishing zones in predicting COTS spatial distribution, yet was slightly more influential for predicting outbreaks. While this finding is contrary to some contemporary thinking (Sweatman 2008, Vanhatalo et al. 2017), these other studies looked primarily at the influence of zoning and did not account for other factors. Importantly these results also provide the first validated estimated of COTS presence, prevalence and outbreak potential across the GBR and provide a useful tool for managers to refine the selection process for prioritizing reefs for COTS control.

As the COTS control program expands and there is increasing spatial and temporal coverage in COTS observation data (see Chapter 3), there is scope to use this modelling framework to provide temporally explicit estimates of the distribution and abundance of COTS. Additionally, this approach may be used to identify the different drivers of primary and secondary outbreaks of COTS. This could provide a way to identify the reefs most likely to experience the gradual build-up of COTS that will initiate the next outbreak cycles. Developing such predictive

frameworks, and integrating them into analytical platforms such as those presented in Chapter 3 is an important step in improving the adaptive management of COTS on the GBR and protecting the remaining coral cover.

7.4 Spatially and temporally explicit simulation modelling for COTS and coral on the GBR

On the GBR there has been increased awareness of the importance of cumulative disturbance on coral reefs (Ortiz et al. 2018, Mellin et al. 2019 - Chapter 5), combined with improved modelling and the collation of the disturbance history of the GBR (Matthews et al. 2019). With this increase in the availability of the necessary data alongside increase of computing power, there has also been a resurgence in the generation of regional scale ecological models for the GBR (Hock et al. 2017, Condie et al. 2018, Mellin et al. 2019a). These models have generally aimed to address three interwoven questions; (1) can we determine the recovery rate of coral reefs and the effects of interacting disturbances (Ortiz et al. 2018, MacNeil et al. 2019); (2) can we use hydrodynamic modelling to identify which reefs are the most influential in terms of spreading COTS outbreaks and/or replenishing degraded reefs through the provision of coral larvae (Hock et al. 2014, 2017); (3) can we recreate the historical trends in coral cover and COTS outbreaks for the GBR (Condie et al. 2018, Mellin et al. 2019 - Chapter 5, Chapter 6). It is important that these lines of research are consolidated into cohesive modelling frameworks that can be applied across the GBR.

Chapter 5 of this thesis uses the predictions of coral growth rate, disturbance response and recovery rate of MacNeil et al. (2015) to predict the growth, disturbance and spatial resilience of GBR reefs in a spatially and temporally explicit fashion. This research recreates the trajectories of coral cover and disturbance which are extrapolated to all reefs on the GBR, providing the first validated estimates of spatial resilience, and importantly the first GBR-wide model for coral growth, disturbance and recovery at a 1km resolution. This research confirms the role that reduced water quality plays in undermining the resilience of coral reefs (Wenger et al. 2016, MacNeil et al. 2019), and provides the first high resolution spatial predictions of

resilience. Most importantly, this research provides a simulation modelling framework that accounts for the spatially explicit disturbance history, abiotic conditions, water quality, coral community composition and coral growth predictions. This framework could be extended to incorporate larval connectivity estimates creating a coupled COTS-Coral metacommunity model for the GBR (Chapter 6).

Within the context of declining coral cover on the GBR, and the urgent need for effective interventions, there has been renewed interest in increasing efficiency of the COTS control program (Fletcher et al. in prep., Westcott et al. 2016, GBRMPA 2017). However, one of the major limitations is the lack of a validated simulation model that can make predictions about the spatial distribution and abundance of COTS. During the last wave of COTS outbreaks, significant advances were made in developing population models for COTS, modelling larval connectivity (Dight et al. 1990a, 1990b) and developing the first metapopulation models for the GBR (Mccallum 1990, Scandol and James 1992, Scandol 1999). However, limited computing power meant that a limited number of reefs (<300) and coarse spatial resolutions (>10km) were necessary. With rapid advances in the hydrodynamic modelling of the GBR (Hock et al. 2014, Thomas et al. 2014, CSIRO 2019) and computing power available to run simulation models, there has been renewed interest in developing simulation models for COTS outbreaks on the GBR. Chapter 6 of this thesis combines the coral growth and recovery model of chapter 5 with contemporary understanding of COTS demography (Pratchett et al. 2014), larval survival (Fabricius et al. 2010, Wolfe et al. 2017, Pratchett et al. 2017b) and larval connectivity estimates (Hock et al. 2014, 2017) to produce a metacommunity model framework for COTS-Coral on the GBR for 1996-2017. This model estimates a time series of chlorophyll concentrations using the relationship ENSO cycles to help drive outbreak patterns in COTS. Importantly, this novel approach is able to recreate general trajectories and timings of COTS outbreaks and the associated loss of coral cover. However, the model was not able to reproduce

the extreme densities of some secondary outbreaks, particularly in the Swains/Townsville regions.

Improvements to the model structure could be made to improve predictions such as incorporating regional estimates of carrying capacity or using available estimates of coral community composition (Mellin et al. 2019 – Chapter 5) to redefine thresholds at which COTS populations collapse. This approach would accommodate the role of preferred prey availability for COTS (*Acropora spp.*) (Pratchett 2007) in promoting severe COTS outbreaks, primarily due to the increased fecundity of adults (Caballes et al. 2016) and viability of larvae (Caballes et al. 2017a). Improved estimates of inter-annual variability of COTS larval connectivity may also help to improve the model fit to empirical time series data, as they have been suggested to be crucially important to the initiation of COTS outbreaks. Additionally, laboratory and modelling research has indicated the importance of temperature gradients in survival of COTS larvae (Lamare et al. 2014, Uthicke et al. 2015b) and the spatial distribution of outbreaks respectively (Chapter 4) and thus, incorporating a temperature component to this model could improve predictions. Importantly, this modelling framework is the first high resolution temporally and spatially explicit simulation model for COTS outbreaks across the GBR, and provides a platform for simulating the effect of a range of proposed management strategies and emerging technologies for COTS control on the GBR.

7.5 Future directions and management implications

The overall objective of this thesis was to provide a range of modelling, visualization and predictive tools for the management of COTS outbreaks within the cumulative disturbance context of the GBR. The development of the COTS Dashboard (Chapter 3) and the CI approach to adaptive management are promising, but could benefit from further improvements. For example the tool, still relies upon some manual upload of data, which could be automated. Furthermore, one of the main objectives of adaptive management is to foster stakeholder engagement which could be further promoted by providing external access to the COTS Dashboard. Developments of GBRMPA's Reef 2050 Integrated Monitoring and Reporting

Program (GBRMPA and Queensland Government 2018) will provide the infrastructure required to both fully automate the Dashboard and provide access to stakeholder groups. Moreover, future development of the modelling frameworks presented in Chapters 4-6 could be integrated into interactive visualisation and analytical tools such as the COTS Dashboard. Such integration could provide enhanced capabilities to make adaptive data driven decisions in terms of prioritizing reefs for culling action or perhaps identifying resilient reefs for enhanced protection. Additionally, integrating these more complex modelling frameworks with easy-to-use interfaces would promote a deeper understanding of the modelling process and appreciation of the associated uncertainty.

Importantly, the modelling frameworks developed in Chapters 4-6 here should continue to be improved by increasing the spatiotemporal resolution of estimates of and understanding of important drivers of COTS distribution. Chapter 6 developed a novel approach to generating time series data for Chlorophyll-*a*, but this approach could be expanded to predict time series for other variables identified in Chapter 4 as important predictors of COTS outbreaks, namely larval connectivity and temperature. Importantly, continued improvements to hydrodynamic and biogeochemical models to create longer time-series at finer resolutions (1km) are essential to improve the accuracy of regional-scale models such as those presented in Chapters 4-6. There also remains a significant gap in understanding surrounding larval predation rates and early life stage mortality of COTS (Pratchett et al. 2017a), to which our model was most sensitive. Future research in this field is essential to reduce model uncertainties and to understand outbreak dynamics.

Results from this thesis highlighted that both water quality and larval connectivity were integral in predicting the spatio-temporal patterns of COTS outbreaks. Importantly, this supports previous hypotheses (Birkeland 1982, Hock et al. 2014, Wooldridge and Brodie 2015) and presents a number of potential management avenues. While ambitious targets for water quality improvements have been set out by the federal and state government (Queensland Government 2018) there is mounting evidence that these goals are unlikely to be met with current measures (Waterhouse et al. 2017) and thus more action is required to improve water quality and reduce

the impact of COTS outbreaks. While larval connectivity cannot be reduced via interventions, the hydrodynamic conditions can be monitored. Ideally existing outputs from hydrodynamic and biogeochemical models coupled with metacommunity (Chapter 6) or distribution models (Chapter 4) could be used to identify the reefs immediately at risk of outbreaks, define prioritization schedules for culling and develop a dedicated early warning system for the development of primary outbreaks. Development of these systems should draw upon important emerging technologies such as early detection of outbreaks via eDNA (Uthicke et al. 2018) or pheromones for aggregation (to make control easier) or dispersion (to decrease fertilisation success) of populations (Hall et al. 2017a). Simulating the effect of management interventions will allow us to identify which (if any) combination of management interventions may be able to stall or diminish the next cycle of COTS outbreaks. In particular, there is a need to be more strategic in the spatial and temporal allocation of management effort, especially given limited resources (Pratchett and Cumming 2019). This thesis builds upon foundational research in this field and provides the necessary tools for improved COTS management and a platform for future development of integrated analytical and simulation tools for the GBR.

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9 Appendix

9.1 Chapter 2 Supplementary Information

Table S 9.1 Identification variables for each of the 15,928 pixels, produced either through GIS software or from definitions given by AIMS (Miller et al. 2009a) or GBRMPA (Great Barrier Reef Marine Park Authority 2001) Reefs are defined by cross shelf location as "inner", "middle", or "outer" as well as they latitudinal sector (Fig S3) Coordinates are defined by the WGS84 Coordinate reference system (EPSG:4326) in decimal degrees.

Column Name	Source	Variable Definition	Unit
PIXEL_ID	GIS	Unique Grid Cell ID	N/A
X		Latitude	Decimal Degrees
Y		Longitude	Decimal Degrees
REEF_ID	GBRMPA	Reef Level ID	Character
REEF_NAME	GBRMPA	Common Reef Name	Character
SECTOR	AIMS	Latitudinal Sector (See Fig S1)	Cape Grenville "CG"; Prince Charlotte Bay "PC"; Cooktown/Lizard Island "CL"; Cairns "CA"; Innisfail "IN"; Townsville "TO"; Cape Upstart "CU"; Whitsundays "WH"; Pompeys "PO"; Swains "SW"; Capricorn Bunker "CB"
SHELF	AIMS	Cross-shelf location	Inner "I"; Middle "M"; Outer "O"

Table S 9.2 Environmental and spatial variables available at a 0.01° spatial resolution for the Great Barrier Reef, comprising the Australia with mean = annual mean levels at the seabed (CARS/GA/ MTSRF/MARS/GEOMACS varaibales) or at the surface (SW/MT variables), seasonal range = a measure of seasonal variability, CARS = CSIRO (Australian Commonwealth Scientific and Industrial Research Organisation) Atlas of Regional Seas (Condie & Dunn, 2006), GA = Geoscience Australia (see Webster & Petkovic, 2005 for original bathymetry dataset), MTSRF = Marine and Tropical Sciences Research Facility (Beaman 2010), MARS = MARine Sediment database (Mathews et al. 2007), GEOMACS = GEological and Oceanographic Model of Australia's Continental Shelf (Hemer, 2006), SeaWiFS = Sea-viewing Wide Field-of-view Sensor (NASA/Goddard Space Flight Center and Orbimage; e.g., Condie & Dunn, 2006), MT = Modis Terra (NASA). K490 is the diffuse attenuation coefficient at wavelength 490nm. Benthic Irradiance (BIR) is estimated from monthly surface photosynthetically active radiation (PAR; Modis) and K490 (SeaWiFS): PAR*exp(-K490*depth) (Kirk 1996).

Column Name	**Source**	**Ref.Code**	**Variable Definition**	**Type**	**Unit**
CRS_NO3_AV	CARS	1-4	Nitrate	mean	µM
CRS_NO3_SR				seasonal range	
CRS_02_AV			Oxygen	mean	$mL.L^{-1}$
CRS_O2_SR				seasonal range	
CRS_PO4_AV			Phosphate	mean	µM
CRS_PO4_SR				seasonal range	
CRS_S_AV			Salinity	mean	PSU
CRS_S_SR				seasonal range	
CRS_SI_AV			Silicate	mean	µM
CRS_SI_SR				seasonal range	
CRS_T_AV			Temperature	mean	^oC
CRS_T_SR				seasonal range	
GA_BATHY	GA	1,5-6	Depth	mean	m
GA_SLOPE			Slope	Degree of slope of seabed	^{o}

GA_ASPECT			Aspect	Degree aspect of slope	^{o}
GBR_BATHY	MTSRF	7	Depth	mean	m
GA_CBRNT	GA/MARS	1, 8-9	Carbonate sediments	mean	%
GA_GRAVEL			Gravel (Ø > 2 mm)	mean	%
GA_SAND			Sand (63 µm < Ø < 2 mm)	mean	%
GA_MUD			Mud (Ø < 63 µm)	mean	%
GMCS_STRESS_TMN	GA/GEOMACS	1,10	Bed shear stress	Trimmed mean	Pa
GMCS_STRESS_IQR				Interquartile range	Pa
SW_CHLA_AV	SeaWiFS	1,11-12	Chlorophyll a	mean	$mg.m^{-3}$
SW_CHLA_SR				seasonal range	
SW_K490_AV		1,13-14	K490 (Turbidity)	mean	m^{-1}
SW_K490_SR				seasonal range	
SW_BIR_AV	SeaWiFS	1,25	Benthic Irradiance	mean	Einsteins $m^{-2}.day^{-1}$
SW_BIR_SR				seasonal range	
MT_SST_AV	Modis Terra (NASA)	1, 15	Sea surface temperature	mean	^{o}C
MT_SST_SR				seasonal range	
MT_SST_MIN				min	

mindistbar	ArcGIS	16	Distance to the coast	Minimum	°
mindistcoa			Distance to the barrier reef	Minimum	°
Primary (representing turbid , sediment dominated plume)	(Devlin et al. 2012a, Alvarez-Romero et al. 2013)	17,18	Primary flood plume frequency (weeks occurred/total weeks) during wet season (max = 26)	Frequency	0-1
Secondary (representing chlorophyll dominated plume)			Secondary flood plume	Frequency	0-1
Tertiary (representing further extent of plume, as delineated by salinity less than 34ppt)			Tertiary flood plume	Frequency	0-1

Table S 9.3 Reference guide for Table S 9.2

Ref.No	Citation
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2	Ridgway, K. R., J. R. Dunn, and J. L. Wilkin. 2002. Ocean interpolation by four-dimensional weighted least squares - Application to the waters around Australasia. Journal of Atmospheric and Oceanic Technology 19:1357–1375.
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15	Huang, Z. 2013. MODIS derived Sea Surface Temperature (SST) datasets. http://www.ga.gov.au/metadata-gateway/metadata/record/gcat_77009.
16	Mellin, C., C. J. a Bradshaw, M. G. Meekan, and M. J. Caley. 2010. Environmental and spatial predictors of species richness and abundance in coral reef fishes. Global Ecology and Biogeography 19:212–222.
17	Devlin, M. J., L. W. McKinna, J. G. Álvarez-Romero, C. Petus, B. Abott, P. Harkness, and J. Brodie. 2012. Mapping the pollutants in surface riverine flood plume waters in the Great Barrier Reef, Australia. Marine Pollution Bulletin 65:224–235.
18	Álvarez-romero, J. G., M. Devlin, E. Teixeira, C. Petus, N. C. Ban, R. L. Pressey, J. Kool, J. J. Roberts, S. Cerdeira-estrada, A. S. Wenger, and J. Brodie. 2013. A novel approach to model exposure of coastal-marine ecosystems to riverine fl ood plumes based on remote sensing techniques. Journal of Environmental Management 119:194–207.
19	https://coralreefwatch.noaa.gov/satellite/coraltemp.php
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24	Sequeira, A. M. M., C. Mellin, H. M. Lozano-Montes, M. A. Vanderklift, R. C. Babcock, M. D. E. Haywood, J. J. Meeuwig, and M. J. Caley. 2016. Transferability of predictive models of coral reef fish species richness. Journal of Applied Ecology 53:64–72.

Table S 9.4 Column properties for DegreeHeatingWeek_data: Annual maximum Degree Heating Weeks (DHW)

Column name	Ref.Code	Variable definition	Units
PIXEL_ID		Unique Grid Cell ID	N/A
lon		Longitude	°
lat		Latitude	°
REEF_ID		Reef Level ID	N/A
annMaxDHW_1985	19	Thermal stress exposure	°C-week
annMaxDHW_1986	19	Thermal stress exposure	°C-week
……		……	…….
annMaxDHW_2017	19	Thermal stress exposure	°C-week

Table S 9.5 Column properties for Bleaching_data_98_02_16.csv: Interpolated values of aerial bleaching scores, 0 (<1% bleached), 1 (1–10% bleached), 2 (10–30% bleached), 3 (30–60% bleached), and 4 (>60% bleached).

Column name	Ref.Code	Variable definition	Units
PIXEL_ID		Unique Grid Cell ID	N/A
lon		Longitude	°
lat		Latitude	°
REEF_ID		Reef Level ID	N/A
bleach_1998	20	Aerial survey score	1-4
bleach_2002	20	Aerial survey score	1-4
bleach_2016	21	Aerial survey score	1-4

Table S 9.6 Column properties for Cyclones_data.csv: Number of hours exposed to waves >4m height/year (4MW)

Column name	Ref.Code	Variable definition	Units
PIXEL_ID		Unique Grid Cell ID	N/A
lon		Longitude	°
lat		Latitude	°
REEF_ID		Reef Level ID	N/A
Hs4MW_1985	22	wave exposure	Hours
Hs4MW_1986	22	wave exposure	Hours
……		……	…….
Hs4MW_2017	22	wave exposure	Hours

Table S 9.7 Column properties for COTS_data.csv: Interpolated A. cf. solaris density per manta tow (A. cf. solaris.manta tow-1)

Column name	Ref.Code	Variable definition	Units
PIXEL_ID		Unique Grid Cell ID	N/A
lon		Longitude	°
lat		Latitude	°
REEF_ID		Reef Level ID	N/A
COTS_1985	23	Interpolated COTS density	COTS.manta tow^{-1}
COTS_1986	23	Interpolated COTS density	COTS.manta tow^{-1}
……		……	…….
COTS_2017	23	Interpolated COTS density	COTS.manta tow^{-1}

9.2 Chapter 4 Supplementary Information

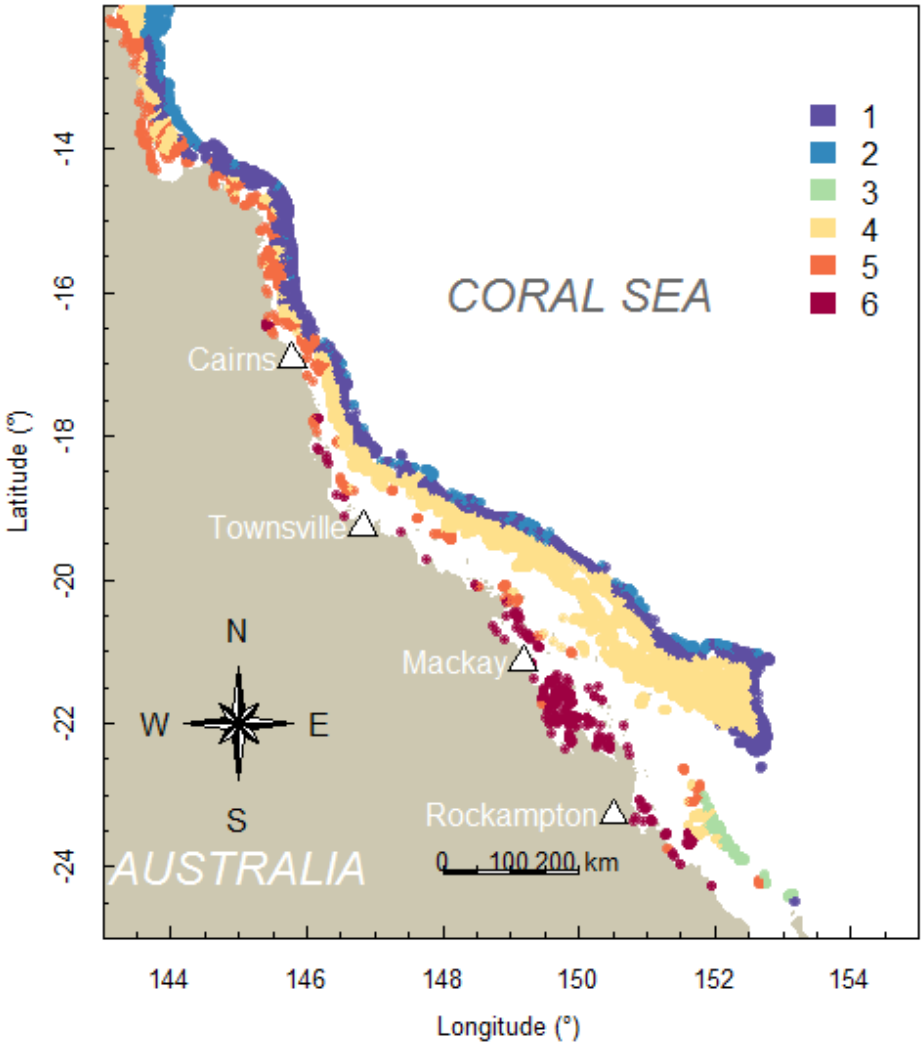

Figure S 9.1 Coral community estimates derived from Mellin et al. (2019). Coral communities represent (1) Outer shelf, soft coral dominated; (2) Outer shelf, digitate coral dominated; (3) Outer shelf, tabulate coral dominated; (4) Middle shelf, mixed community; (5) Inner shelf, *Porites* dominated and (6) Inner shelf, macroalgae dominated

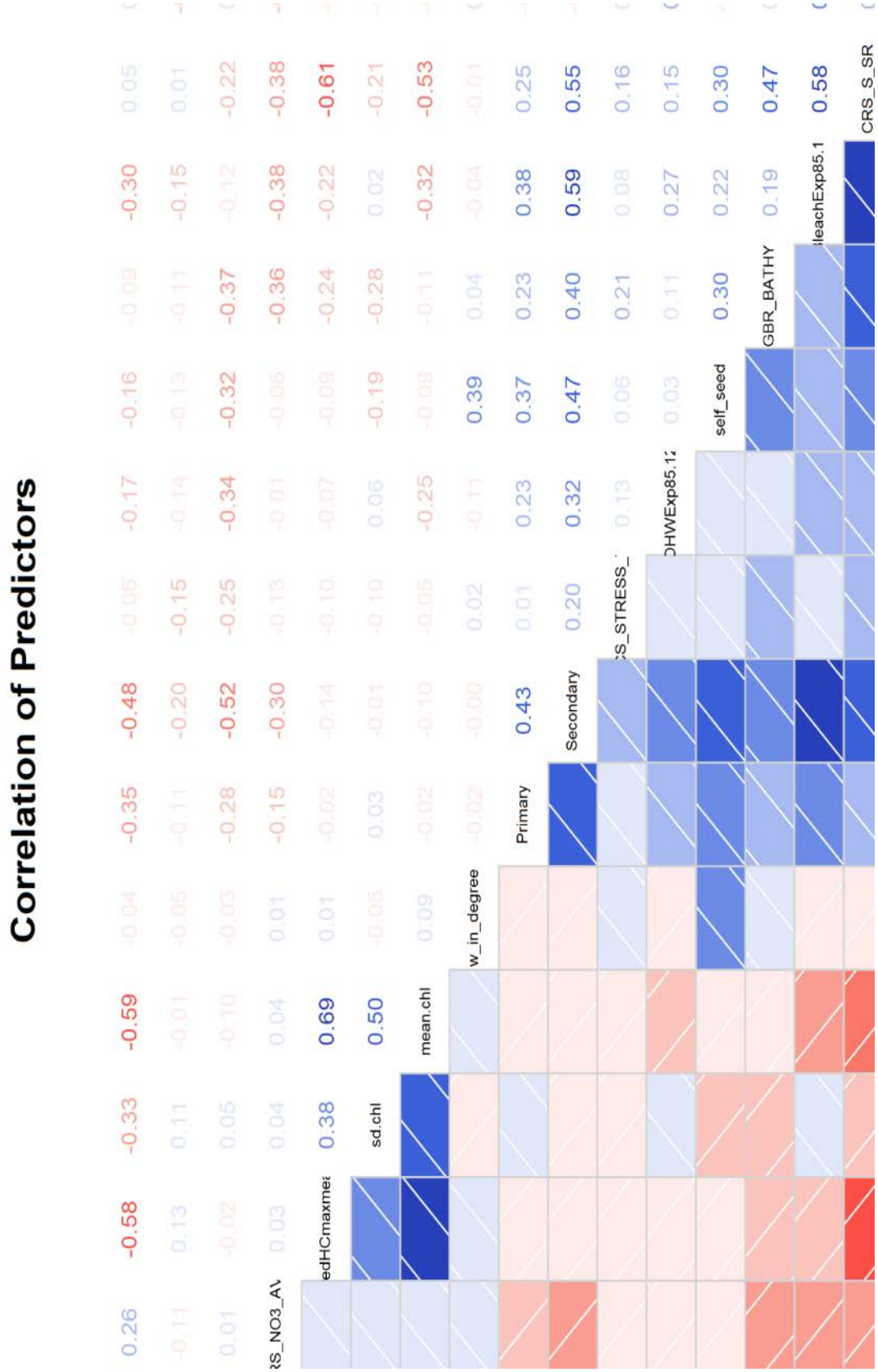

Figure S 9.2 Pearson correlation values for all predictors. Red indicates a negative correlation, while blue indicates positive.

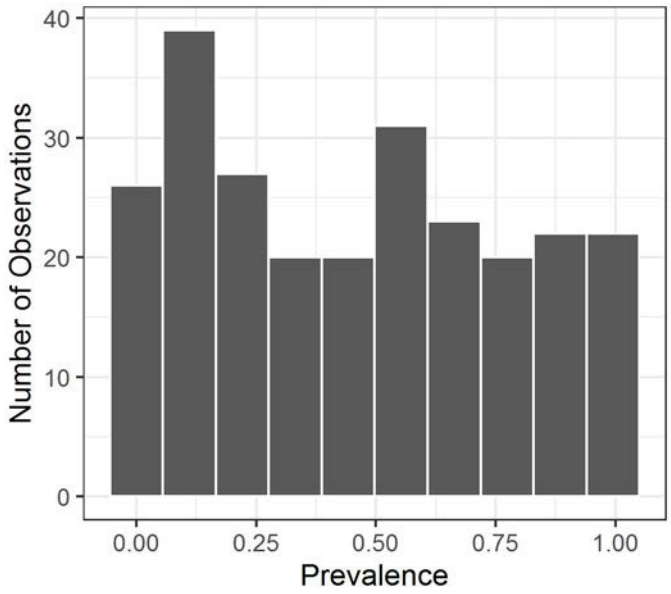

Figure S 9.3 Histogram of prevalence values (maximum proportion of manta tows in which COTS were observed) across all calibration data, excluding zero value.

9.3 Chapter 5 Supplementary Information

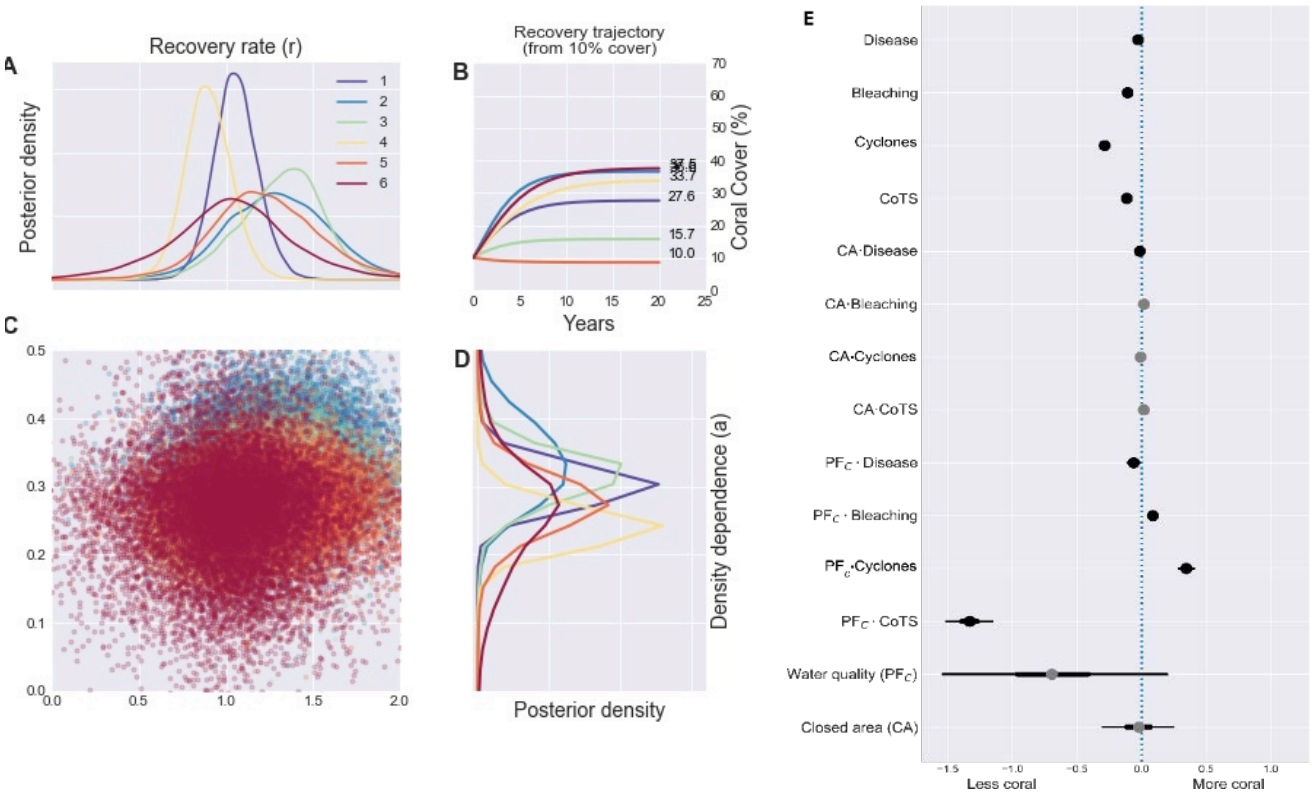

Figure S 9.4 Bayesian parameter estimates from a Gompertz-based mechanistic model of coral cover growth among AIMS long-term monitoring program (AIMS LTMP) reefs (n=46) on the Great Barrier Reef (GBR). A) Posterior distribution of intrinsic rate of increase (*r*) among benthic communities; B) median predicted recovery trajectories from 10% initial cover for GBR benthic communities, in the absence of coral loss from disturbance; C) scatterplot of joint posterior samples for model *r* (intrinsic rate of increase) and *a* (density dependence) Gompertz-based coral model parameters, where axis labels in A) and D) apply; D) posterior distribution of *a* among benthic communities; and E) posterior effect size plot for Gompertz-based coral model covariate parameters, including posterior medians (circle), 50% uncertainty intervals (thick line), and 95% uncertainty intervals (thin line), with grey dots indicating parameters where the 95% UI overlaps zero, and black dots where they do not. Benthic communities are coded as 1 (*Out- Soft*): Outer shelf communities characterized by soft corals; 2 (*Out- Digit*)*:* Outer shelf communities characterized by *Acropora* digitate (among others); 3 (*Out-tab*): Outer shelf communities characterized by *Acropora* tabular (among others); 4 (*Mid- mixed*): mid shelf mixed communities; 5 (*In- Porites*): inner shelf communities characterized by *Porites* (among others); 6 (*In-MA*): inner shelf communities characterized by macroalgae (among others).

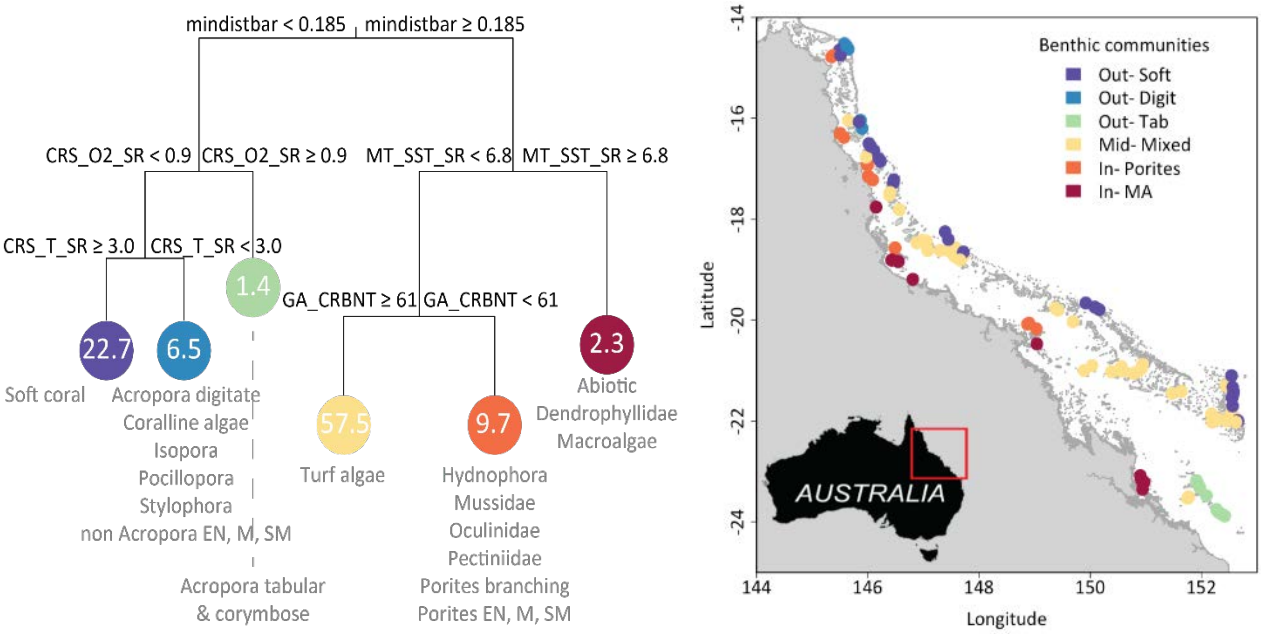

Figure S 9.5 Multivariate regression tree of benthic communities. Left: six benthic communities were defined by splitting all survey reefs (N = 110) based on environmental predictors. Numbers represent the proportion of each community on the GBR (%) and corresponding indicator taxa. Right: Map of survey reefs and corresponding benthic communities. With mindistbar: minimum distance to the barrier reef edge, CRS_O2_SR: seasonal range in seabed oxygen concentration, CRS_T_SR: seasonal range in seabed temperature, MT_SST_SR: seasonal range in sea surface temperature, GA_CRBNT: % carbonate sediments, Out- Soft: Outer shelf communities characterized by soft corals; Out- Digit: Outer shelf communities characterized by Acropora digitate (among others); Out- tab: Outer shelf communities characterized by Acropora tabular (among others); Mid- mixed: mid shelf mixed communities; In- Porites: inner shelf communities characterized by Porites (among others); In-MA: inner shelf communities characterized by macroalgae (among others).

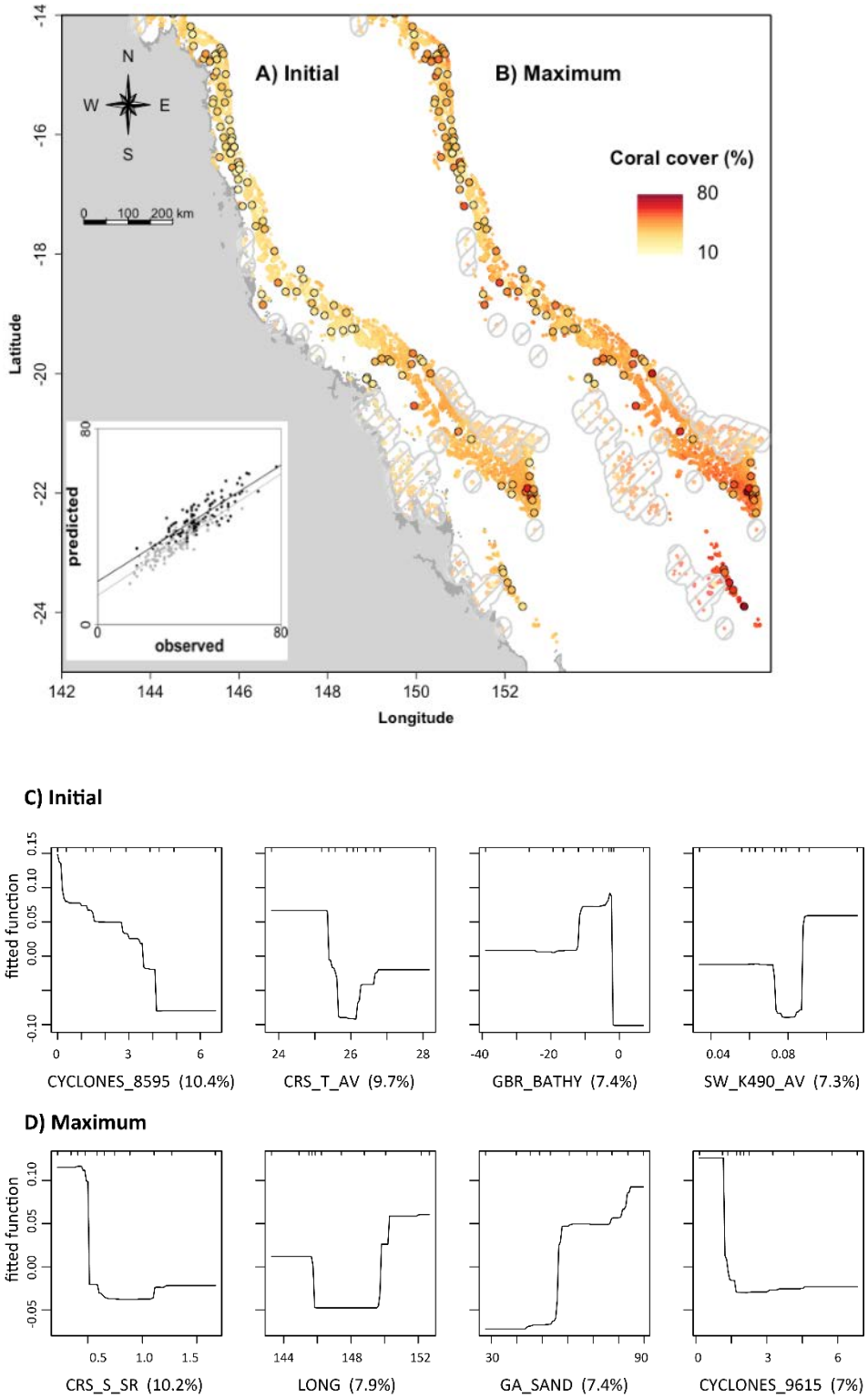

Figure S 9.6 Boosted regression trees of initial and maximum coral cover. Top: predicted spatial patterns in initial (A) and maximum (B) coral cover. Dots represent observed values for survey reefs used for model calibration. The insert shows the relationship between manta observations and BRT predictions for initial (grey) and maximum (black) coral cover. The dashed areas indicate lower confidence in model predictions due to extrapolation. Bottom: Partial effects for boosted regression trees predicting initial coral cover (C) and maximum coral cover (D). The relative importance of each predictor (%) is indicated in brackets. With CYCLONES_8595: total duration of destructive waves (>4m)

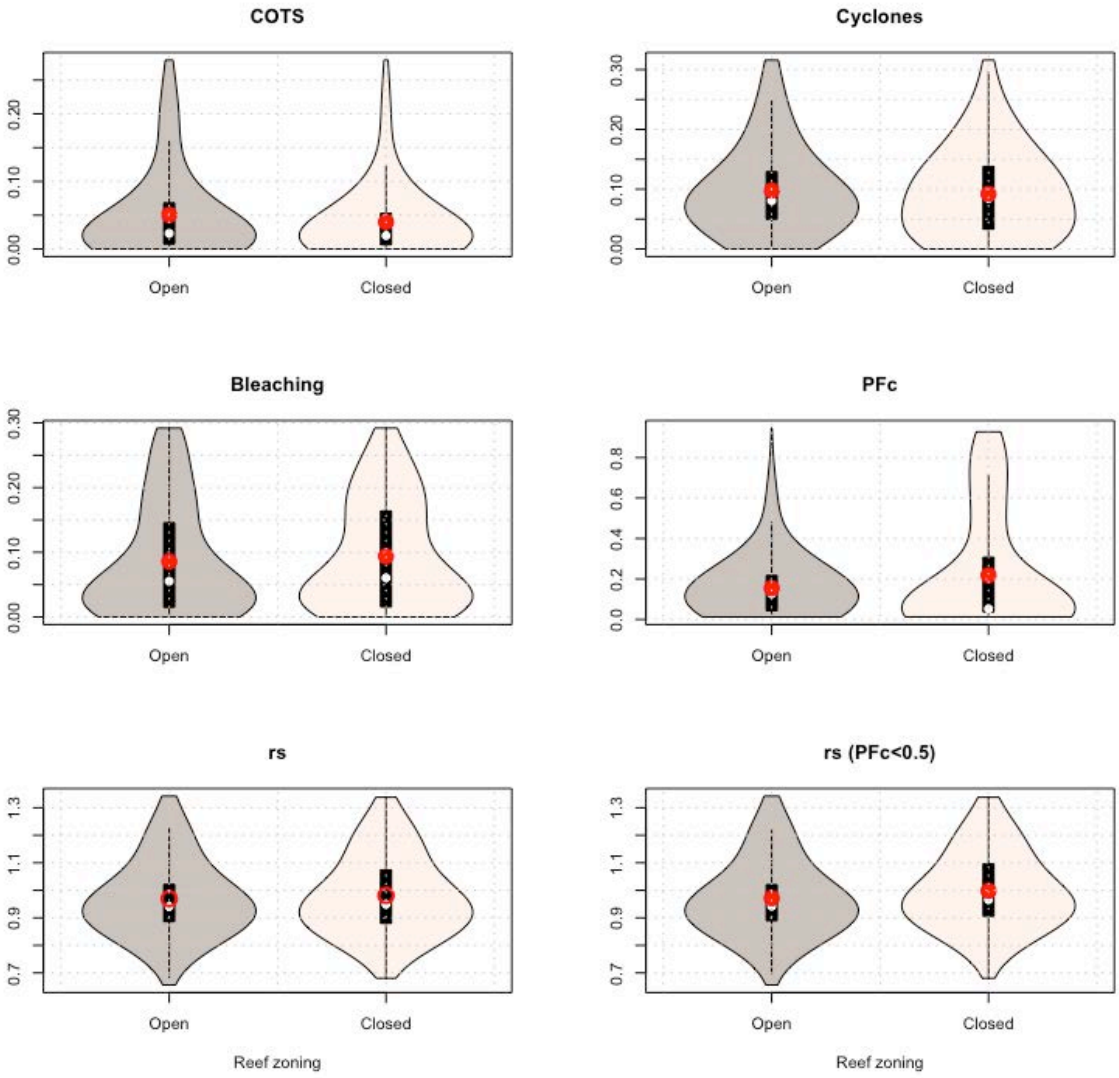

Figure S 9.7 Distribution of disturbance impacts, water quality and coral growth rate on reefs within or outside no-take marine protected areas. With PFc: frequency of river plume conditions and rs: coral intrinsic growth rate. The white dot indicates the median, the vertical black bar the interquartile range, and plot width represents the proportion of all reefs. The red dot indicates the mean, with closed dots showing significantly different means between open and closed (i.e. no-take) reef areas (Kruskal-Wallis test, $P < 0.001$).

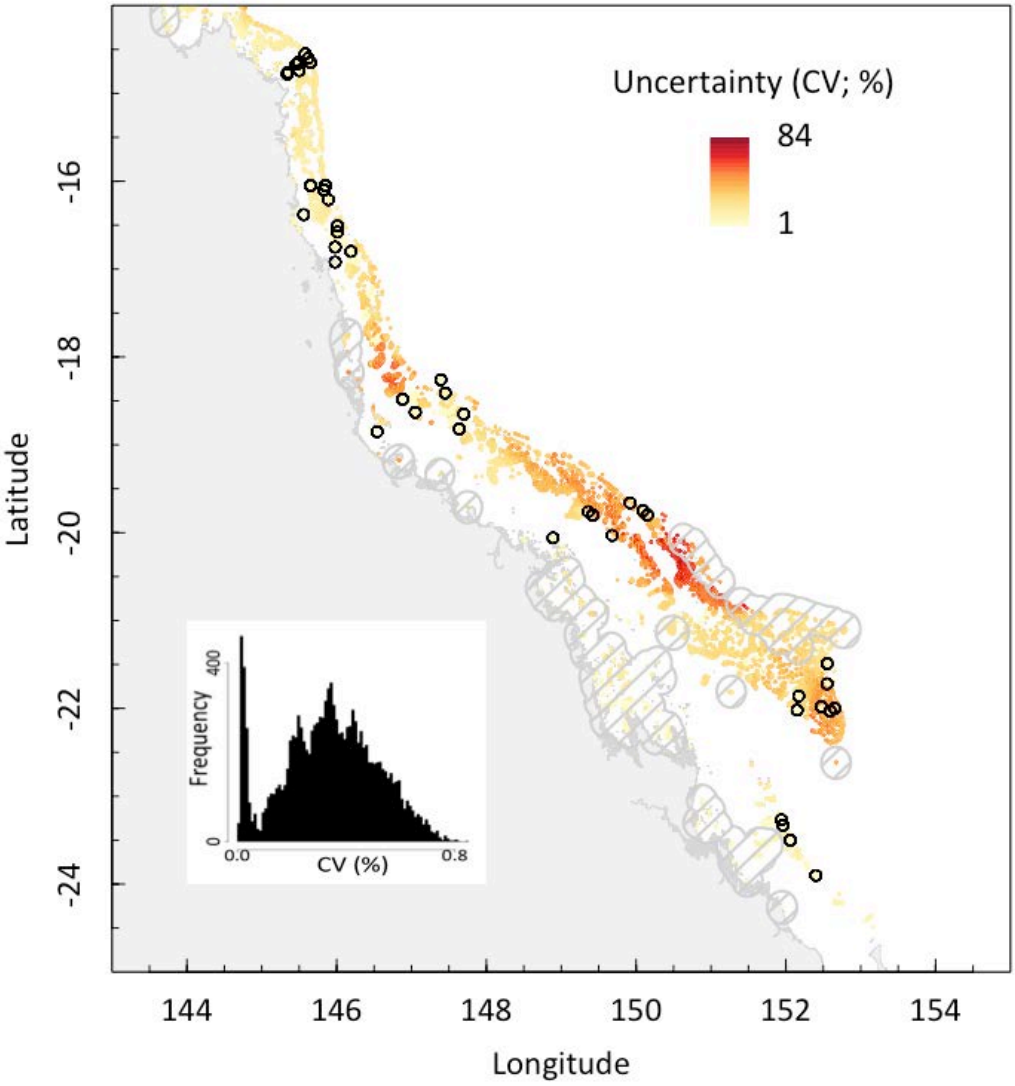

Figure S 9.8 Model uncertainty. Uncertainty is expressed as the coefficient of variation (CV; %) in model predictions among a total of 1,000 simulations. Dots show reefs surveyed by the long-term monitoring program used for calibrating the Gompertz model. The dashed areas indicate lower confidence in model predictions due to extrapolation.

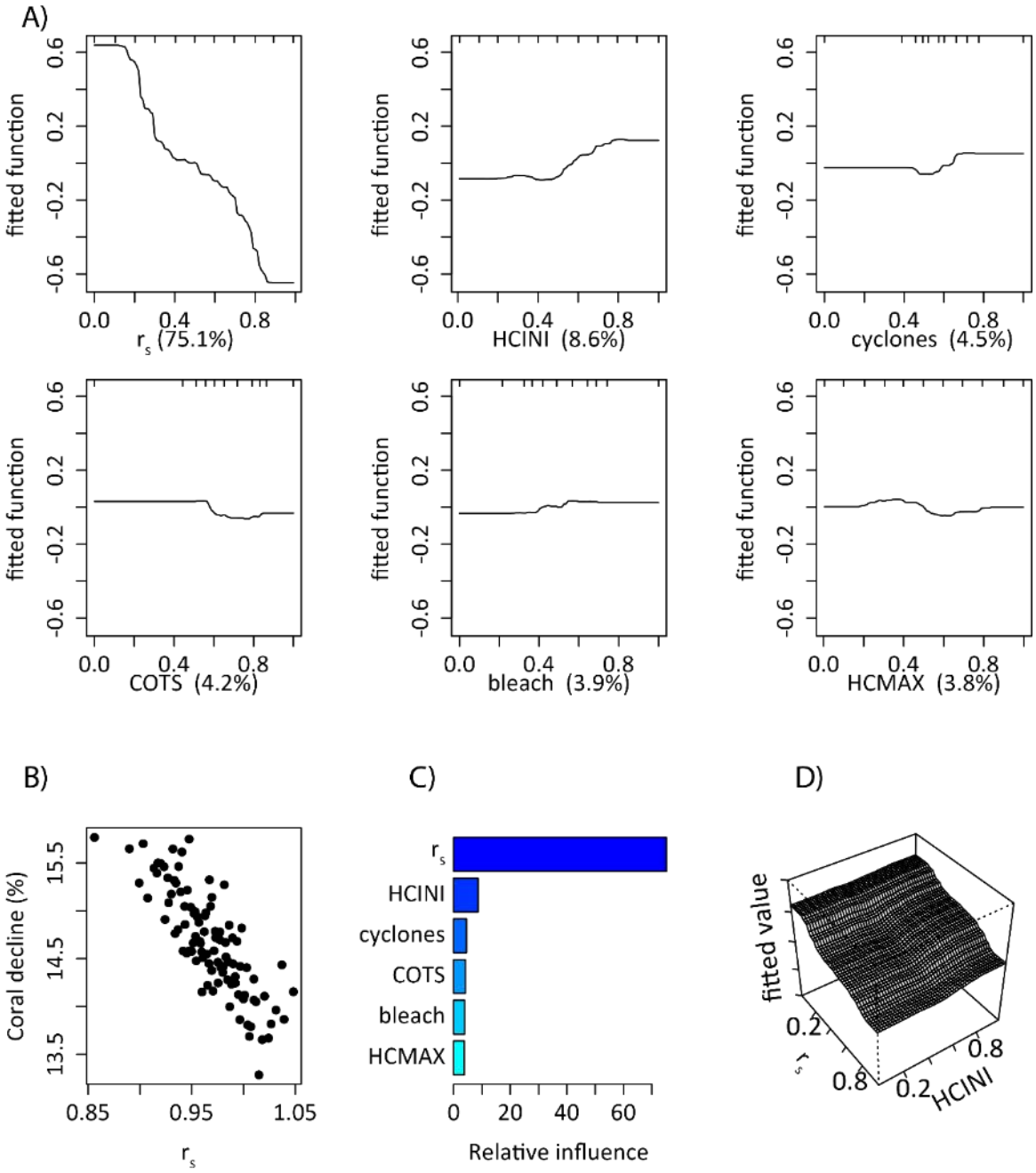

Figure S 9.9 Sensitivity analysis. (A) Boosted regression tree partial effects showing the relationship between each model parameter and the extent of predicted coral decline across the Great Barrier Reef. The relative importance (%) of each model parameter is indicated in brackets. (B) Scatter plot showing the mean extent of predicted coral decline across the Great Barrier Reef (%) as a function of the mean coral growth rate ($\boldsymbol{r_s}$). (C) Relative influence (%) of each model parameter on predicted coral decline across the Great Barrier Reef. (D) Interactive effect of $\boldsymbol{r_s}$ and initial coral cover (*HCINI*) on the extent of predicted coral decline. With *cyclones*: total cyclone severity from 1996 to 2017, *COTS*: total density of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) from 1996 to 2017, *bleach*: total bleaching severity from 1996 to 2017, *HCMAX*: maximum coral cover from 1996 to 2017

Table S 9.8 Environmental and spatial variables considered as candidate predictors and available at a 0.01º spatial resolution for the Great Barrier Reef, Australia. With mean = annual mean levels, std dev = standard deviation in monthly mean levels, as a measure of seasonal variability, CARS = CSIRO (Australian Commonwealth Scientific and Industrial Research Organisation) Atlas of Regional Seas (1), GA = Geoscience Australia (see Webster & Petkovic (2) for original multibeam bathymetry dataset), MARS = MARine Sediment database (3), SeaWiFS = Sea-viewing Wide Field-of-view Sensor (NASA/Goddard Space Flight Center and Orbimage (1)). K490 is the diffuse attenuation coefficient at wavelength 490 nm.

Variable	Source	Definition	Type	Unit	Justification
CRS_NO3_AV _SR	CARS	Nitrate	mean std dev	µM	Affects coral physiology, growth and calcification rates (4, 5)
CRS_PO4_AV _SR		Phosphate	mean std dev	µM	Affects coral physiology, growth and calcification rates (4, 5)
CRS_O2_AV _SR		Oxygen	mean std dev	$mL.L^{-1}$	Affects coral calcification rates (6); oxygen depletion characteristic of eutrophic conditions (4)
CRS_S_AV _SR		Salinity	mean std dev	PSU	Decreases with terrestrial runoff and freshwater input (4), influences coral calcification (7) and reproduction (8)
CRS_T_AV _SR		Seabed temperature	mean std dev	ºC	Influences metabolic rates; determines species distribution through thermal tolerance thresholds (9)
MT_SST_AV _SR	Modis Terra (NASA)	Sea surface temperature	mean std dev	ºC	Influences metabolic rates; determines species distribution through thermal tolerance thresholds (9)
SW_CHL_AV	SeaWIFS	Chlorophyll a	mean	$mg.m^{-3}$	Quantifies primary productivity and eutrophic conditions affecting coral ecophysiology (4)

_SR			std dev		
SW_K490_AV _SR		K490 (Turbidity)	mean std dev	m^{-1}	Reflects light availability in support of photosynthesis (4)
GBR_BATHY	MTSRF	Depth	mean	m	Determines light availability and co-varies with other variables (e.g. temperature, salinity, nutrient availability) (10)
GA_CBRNT	GA/MARS	Carbonate sediments	mean	%	Increases available substrate and carrying capacity (10, 11)
GA_SAND		Sand (63 µm < Ø < 2 mm)	mean	%	Decreases available substrate and carrying capacity (10, 11)
mindistbar	ArcGIS	Distance to the barrier reef edge	Minimum	°	Provides a proxy for cross-shelf gradient shared among multiple environmental covariates (9, 10)
mindistcoa		Distance to the coast	Minimum	°	Provides a proxy for cross-shelf gradient shared among multiple environmental covariates (9, 10)
PFc	Modis	Flood plume frequency during wet season	Frequency	0-1	Influences coral growth rate (12)

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Table S 9.9 Survey reefs and sample size used at each model development step. With MRT: multivariate regression trees; HLM: hierarchical linear model; BRT: boosted regression trees; r_s: intrinsic coral growth rate; HC_{ini}: initial coral cover; HC_{max}: maximum coral cover; AIMS LTMP: Long-term monitoring program; MMP: marine monitoring program; RAP: representative areas program (see Methods for details).

Step	**AIMS LTMP**	**Manta**	**MMP**	**RAP**	**Rationale**
MRT (Benthic communities)	46		17	45	Increase spatial coverage and representation of inshore reefs
Bayesian HLM (r_s)	46				Coral cover available at the transect level
BRT (r_s)	46				Estimates from Bayesian HLM
BRT (HC_{ini})	46	62			Increase spatiotemporal coverage and sample size
BRT (HC_{max})	46	62			Increase spatiotemporal coverage and sample size
Out-of-sample validation of predicted coral cover trajectories		10			Reefs not used for model calibration with available disturbance history

9.4 Chapter 6 Supplementary Information

Table S 9.10 Nino 3.4 Index used to predict chlorophyll concentrations between 1996-2017. The September October-November (SON) values *(Rayner et al. 2003)* were used to model this relationship. Values coloured in blue represent La Niña periods and those in red represent El Niño events

Year	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON	OND	NDJ
1996	-0.9	-0.8	-0.6	-0.4	-0.3	-0.3	-0.3	-0.3	-0.4	-0.4	-0.4	-0.5
1997	-0.5	-0.4	-0.1	0.3	0.8	1.2	1.6	1.9	2.1	2.3	2.4	2.4
1998	2.2	1.9	1.4	1	0.5	-0.1	-0.8	-1.1	-1.3	-1.4	-1.5	-1.6
1999	-1.5	-1.3	-1.1	-1	-1	-1	-1.1	-1.1	-1.2	-1.3	-1.5	-1.7
2000	-1.7	-1.4	-1.1	-0.8	-0.7	-0.6	-0.6	-0.5	-0.5	-0.6	-0.7	-0.7
2001	-0.7	-0.5	-0.4	-0.3	-0.3	-0.1	-0.1	-0.1	-0.2	-0.3	-0.3	-0.3
2002	-0.1	0	0.1	0.2	0.4	0.7	0.8	0.9	1	1.2	1.3	1.1
2003	0.9	0.6	0.4	0	-0.3	-0.2	0.1	0.2	0.3	0.3	0.4	0.4
2004	0.4	0.3	0.2	0.2	0.2	0.3	0.5	0.6	0.7	0.7	0.7	0.7
2005	0.6	0.6	0.4	0.4	0.3	0.1	-0.1	-0.1	-0.1	-0.3	-0.6	-0.8
2006	-0.8	-0.7	-0.5	-0.3	0	0	0.1	0.3	0.5	0.7	0.9	0.9
2007	0.7	0.3	0	-0.2	-0.3	-0.4	-0.5	-0.8	-1.1	-1.4	-1.5	-1.6
2008	-1.6	-1.4	-1.2	-0.9	-0.8	-0.5	-0.4	-0.3	-0.3	-0.4	-0.6	-0.7
2009	-0.8	-0.7	-0.5	-0.2	0.1	0.4	0.5	0.5	0.7	1	1.3	1.6
2010	1.5	1.3	0.9	0.4	-0.1	-0.6	-1	-1.4	-1.6	-1.7	-1.7	-1.6
2011	-1.4	-1.1	-0.8	-0.6	-0.5	-0.4	-0.5	-0.7	-0.9	-1.1	-1.1	-1
2012	-0.8	-0.6	-0.5	-0.4	-0.2	0.1	0.3	0.3	0.3	0.2	0	-0.2
2013	-0.4	-0.3	-0.2	-0.2	-0.3	-0.3	-0.4	-0.4	-0.3	-0.2	-0.2	-0.3
2014	-0.4	-0.4	-0.2	0.1	0.3	0.2	0.1	0	0.2	0.4	0.6	0.7
2015	0.6	0.6	0.6	0.8	1	1.2	1.5	1.8	2.1	2.4	2.5	2.6
2016	2.5	2.2	1.7	1	0.5	0	-0.3	-0.6	-0.7	-0.7	-0.7	-0.6
2017	-0.3	-0.1	0.1	0.3	0.4	0.4	0.2	-0.1	-0.4	-0.7	-0.9	-1
2018	-0.9	-0.8	-0.6	-0.4	-0.1	0.1	0.1	0.2	0.4	0.7	0.9	0.8

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Modelling Growth of Juvenile Crown-of-Thorns Starfish on the Northern Great Barrier Reef

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Abstract: The corallivorous crown-of-thorns starfish (*Acanthaster* spp.) is a major cause of coral mortality on Indo-Pacific reefs. Despite considerable research into the biology of crown-of-thorns starfish, our understanding of the early post-settlement life stage has been hindered by the small size and cryptic nature of recently settled individuals. Most growth rates are derived from either laboratory studies or field studies conducted in Fiji and Japan. The Great Barrier Reef (GBR) is currently experiencing its fourth recorded outbreak and population models to inform the progression of outbreaks lack critical growth rates of early life history stages. High numbers of 0+ year juveniles (n = 3532) were measured during extensive surveys of 64 reefs on the northern GBR between May and December 2015. An exponential growth model was fitted to the size measurement data to estimate monthly ranges of growth rates for 0+ year juveniles. Estimated growth rates varied considerably and increased with age (e.g., 0.028–0.041 mm·day^{-1} for one-month-old juveniles versus 0.108–0.216 mm·day^{-1} for twelve-month-old juveniles). This pioneering study of 0+ year juveniles on the GBR will inform population models and form the basis for more rigorous ongoing research to understand the fate of newly settled *Acanthaster* spp.

Keywords: juvenile crown-of-thorns starfish; growth rates; growth curve analysis

1. Introduction

Crown-of-thorns starfish (*Acanthaster* spp.) are among the most intensively studied of all coral reef organisms [1]. This starfish species is renowned for its extreme temporal and spatial variation in abundance, which can result in extensive destruction of coral reef habitats if starfish occur at high densities (during outbreaks). Outbreaks of crown-of-thorns starfish are considered to be one of the foremost causes of significant and sustained declines in live hard coral cover on Indo-Pacific reefs [2–5]. On Australia's Great Barrier Reef (GBR), there have been four distinct episodes of outbreaks since the early 1960's, with the latest outbreak first apparent in 2010 [6,7]. Over a period of 27 years (1985 to 2012), the GBR has lost approximately half of its initial coral cover, with 42% of this loss attributable to recurrent outbreaks of crown-of-thorns starfish [2].

Outbreaks of crown-of-thorns starfish are fundamentally caused by changes in key demographic rates and population dynamics [8], resulting in either progressive accumulation of starfish over several successive cohorts [9] or the rapid onset of outbreaks following a single mass-recruitment event [10]. However, the extent to which these demographic changes are caused by anthropogenic degradation of reef ecosystems (e.g., overfishing and/or eutrophication) versus inherent environmental changes and stochasticity (e.g., cycles of food availability for larvae, juveniles, and/or adult starfish)

is largely unknown and widely debated [6,11]. Our understanding of the proximal and ultimate causes of outbreaks has been hampered at least in part by difficulties in studying the early life stages of crown-of-thorns starfish in natural environments [6,11]. Current models [7,12,13] that aim to understand and predict outbreak dynamics lack critical demographic rates, such as estimates of growth rates and survival for early life history stages in the field.

Field-based studies of early life stages of crown-of-thorns starfish have largely been constrained by the small size, cryptic nature, and largely nocturnal habits of recently settled individuals [10], making them difficult to detect and sample [14–16]. Attempts to locate 0+ year old juveniles on the GBR have remained largely unsuccessful [14–16]. However, studies conducted in Fiji and Japan that followed individual cohorts of crown-of-thorns starfish through time on single island reefs effectively sampled newly settled individuals (0+ year old) [10,17]. Resulting estimates of growth rates for coralline algae feeding juveniles (2–3 mm/month) [10,17] were consistent with early post-settlement growth estimates for laboratory reared juveniles [18,19].

As early stages of newly settled juveniles (i.e., 1–3 months-old starfish after settlement, size = 0.3–5 mm) have rarely been detected in the field [17], demographic rates for these early stages are largely derived from aquarium-based studies [18,19]. Crown-of-thorns starfish have been reared in captivity since 1973, providing important insights into their early development and life history [18–21]. Once fully developed competent larvae (i.e., at the late brachiolaria stage) find a suitable settlement substrate (i.e., coralline algae), they metamorphose within two days into five-armed juvenile starfish that measure between 0.3 and 0.8 mm in diameter [18,19,22,23]. Yamaguchi (1973) [18] found that laboratory-reared juveniles grew 0.076 mm·day^{-1} in the 20 weeks following settlement, while Lucas (1974) [19] estimated that 3-month-old juveniles grew 0.048 mm·day^{-1} in the laboratory. Field-based estimates of juvenile growth rates averaged 0.10–0.15 mm·day^{-1} in the coralline algae feeding phase and 0.40–0.84 mm·day^{-1} in the coral feeding phase [10,17]. So far, existing growth data has been fitted with logistic or Gompertz growth equations to describe the sigmoidal growth pattern of crown-of-thorns starfish [10,17,20,21,24]. However, these equations have been acknowledged to be limited in accurately describing growth during distinct life stages [21], and so alternative equations have been suggested for distinct stages, such as for coralline algae feeding juveniles [25] and coral-eating 1+ year old juveniles [21,26].

The purpose of this study was to reconstruct growth curves for juvenile (0+ year old) crown-of-thorns starfish on the northern GBR, based on intensive (near monthly) field sampling of newly settled individuals. The exact ages of juvenile starfish cannot be verified, but may be inferred for 0+ year old starfish by assuming that settlement occurs within a relatively narrow period [10,17]. Here we provide, for the first time, monthly ranges of growth rates for 0+ year juveniles to inform crown-of-thorns starfish population models. In addition, we compare these results to previous field studies and present ranges of predicted mean sizes for different age classes that can be used to inform the planning of future juvenile monitoring studies on the GBR.

2. Materials and Methods

2.1. Field Collection

All field sampling was conducted in conjunction with the Association of Marine Park Tourism Operators' (AMPTO) crown-of-thorns starfish control vessels during the fourth recorded outbreak of *Acanthaster* cf. *solaris* [27] on Australia's GBR. One hundred and eleven sites on 64 reefs within six geographic locations (or reef complexes) located between 14.72° S and 17.67° S were sampled between 7 May and 15 December 2015 (Figure 1). At each site, 1–2 SCUBA divers searched coralline algae encrusted pieces of dead coral and live coral colonies for juvenile crown-of-thorns starfish and their feeding marks. Individual pieces of live and dead coral were thoroughly inspected for juvenile starfish if feeding marks were sighted on exposed surfaces. Each diver was able to cover up to 250 m^2 during a typical 40 min dive. However, if juvenile abundances were high (e.g., 40 individuals collected

during a 40 min dive), search effort was restricted to a much smaller area (≈50 m^2). All starfish (target size ≤ 50 mm) were collected and placed in sampling jars underwater. This size threshold was selected, as previous growth models [17,21,24] predict that the mean size of starfish from the previous year's cohort would be >50 mm at the time of our first sampling (May 2015). The size of individuals was not measured in situ, and as such, two of the 3532 juveniles were slightly larger than 50 mm (52.5 mm and 64 mm). These larger individuals were collected in November/December 2015, and were retained in the analysis, as they were likely to have come from the same cohort. After each sampling dive, juvenile starfish were kept alive in containers filled with seawater, and their maximum diameter was measured to the nearest half millimetre with a stainless steel ruler. Once starfish were measured, all individuals were preserved in 95% ethanol for future analyses.

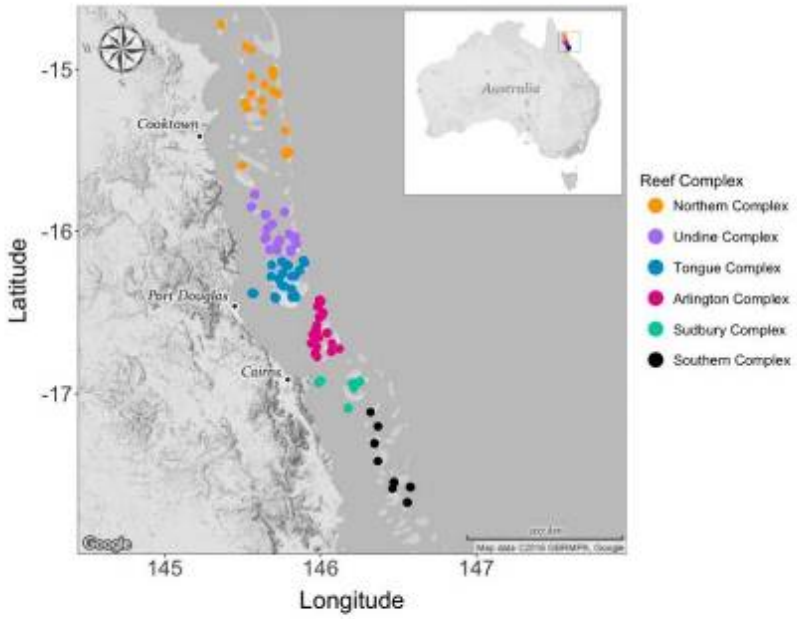

Figure 1. Map of the north Queensland coast showing the sampling locations (n = 111) and designated reef complexes (n = 6) for the collection of 0+ year crown-of-thorns starfish.

2.2. *Growth Curve Analysis*

On the GBR, spawning has been reported to occur throughout summer months, but is concentrated in December and January [6]. In the year of sampling, Uthicke et al. (2015) [28] reported that spawning occurred between 10 and 21 of December 2014 in the area of the northern GBR relevant to our study (i.e., 1 to 7 days prior to sampling), and that there was no subsequent spawning throughout December or January. Assuming a planktonic larval duration of 10 to 40 days [22,23,29–32], settlement is likely to have occurred predominantly—if not exclusively—in early January 2015. As age of sampled individuals cannot be verified, age of sampled juveniles for the model was based on the assumption that all juveniles settled on 1 January 2015 (i.e., 10–21 days after the reported spawning, which incorporates the 17–22 peak settlement window determined by Pratchett et al., in review [33]). Ultimately, all growth estimates are presented as monthly growth rates, and so even if crown-of-thorns starfish settled over several days to weeks, it would have limited influence on our results.

All exploratory and growth curve analyses were conducted using R [34]. A series of preliminary models (e.g., logistic growth model and exponential growth model) were fitted to the 2015-juvenile size data to determine which type of model was most suitable to describe the relationship between size and age. Visual inspection and exploratory analysis of the fitted growth curves (based on least residual sum of squares) identified an exponential growth model (as suggested by Okaji (1996) [25]) in the following form as the most accurate in describing the shape of the size measurement data:

$$Size_{Age} = \beta_0 \times e^{k \times Age} + \beta_1 \quad \text{(m1)}$$

where *Size* is the diameter of starfish in mm, *Age* is number of days since 1 January, and β_0, k, and β_1 are parameters to be estimated. As size measurements were missing for the initial four months of development (i.e., sampling period: January to April 2015), the y-intercept (i.e., $Size_{Age=0}$) was fixed to a biologically meaningful size (see below), representative of the range of predicted mean sizes for newly metamorphosed juvenile starfish in the laboratory ([23]; see Appendix A, Table A1). The growth model may therefore be represented as:

$$Size_{Age} = \beta_0 \times e^{k \times Age} + (Size_{Age=0} - \beta_0) \quad \text{(m2)}$$

Three estimates of size after metamorphosis (i.e., $Size_{Age=0}$ = 0.30 mm, 0.56 mm, and 0.82 mm) from Fabricius et al. (2010) [23] were used to generate three different *m2* models ($m2_{Size\ at\ Age0=0.30}$, $m2_{Size\ at\ Age0=0.56}$, $m2_{Size\ at\ Age0=0.82}$). Best-fit parameter estimates for *m1* (β_0, k, and β_1) and *m2* (β_0, k) models were obtained with associated 95% confidence intervals using the *nlstools* package [35]. Residuals from the preliminary models were found to display a distinct wedge pattern, indicating that variance was related to age of juveniles, and thus multiple variance functions (Age^2, Age^3, Age^4) were trialled to optimize best-fit parameter estimates for each model (*m1*, $m2_{Size\ at\ Age0=0.30}$, $m2_{Size\ at\ Age0=0.56}$, $m2_{Size\ at\ Age0=0.82}$). Best-fit parameter estimates for all 12 models were then used to perform linear mixed effect analysis of the relationship between *Size* and *Age* using the *nlme* package [36]. Reef complex and survey sites were included in the linear mixed effect models as nested random factors to account for variation at the site and reef complex scale, and variance structures (Age^2, Age^3, Age^4) were included to account for the variation in size with age. Best-fit models were selected based on lowest Akaike Information Criterion (AIC). No evidence of spatial autocorrelation was found after both visual (variograms and bubble plots) and statistical inspection (incorporating spatial correlation structures into mixed effects models).

A selection of best-fit models and corresponding 95% confidence intervals was then plotted using the *ggplot2* package [37]. The best-fit model of $m2_{Size\ at\ Age0=0.56}$ was plotted with the upper bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.82}$ and the lower bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.30}$, forming a so-called "combined 95% confidence interval". Growth rates (i.e., growth increment per unit time) were calculated for different time spans (i.e., 30-day intervals) for the upper bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.82}$, and the lower bound of the 95% confidence interval of $m2_{Size\ at\ Age0=0.30}$ to provide ranges of modelled growth rates.

3. Results

Size ranges of juvenile starfish increased as sampling progressed through the year (Figure 2a). Juveniles sampled in May measured between 3 and 15.5 mm in size (size range = 12.5 mm), while those sampled in December ranged from 8.5 to 52.5 mm (size range = 44 mm) (Figure 2a), representing a 3.5-fold increase in size range within this time period.

For *m1* models (variable intercept), growth was indeed exponentially related to age (t_{3420} = 59.79, $p < 0.0001$), while including *site* ($\sigma \approx 0.0007$) and *reef complex* ($\sigma \approx 0.0003$) as random factors. Best model performance was achieved with a variance structure of Age^3 (AIC = 18,057), indicating that variance increased cubically with age. However, the best-fit *m1* model predicted mean size after metamorphosis ($Size_{Age=0}$) to be 5.42 mm. This appears to be erroneous, as it is in stark contrast with the range of

expected mean sizes for newly settled juveniles (i.e., 0.30–0.82 mm). Consequently, the *m2* models seemed to describe growth more accurately because their intercept was fixed to a biologically relevant size after metamorphosis. Again, for *m2* models (fixed intercept), growth was indeed exponentially related to age ($m2_{Size\ at\ Age0=0.82}$, $t_{3420} = 59.55$, $p < 0.0001$), and a variance structure of Age^3 gave the best model performance ($m2_{Size\ at\ Age0=0.82}$, AIC = 18,071). Although overall model performance was slightly reduced using the fixed intercept models (based on a higher AIC), fixing the intercept to a biologically meaningful size provides a better characterisation of the growth curves for juvenile crown-of-thorns starfish.

The growth curve analysis highlights increasing variation in size among older individuals. As shown by the distribution of size–frequency data for different sampling periods (Figure 2a) and the gradual widening of the combined 95% confidence interval (Figure 2b), variance increased considerably as juveniles grew older. The increased variation in size with age was further reflected by the increase of monthly ranges of modelled growth rates (Table 1). Ranges of modelled growth rates increased from 0.028–0.041 mm·day^{-1} for one-month-old juveniles to 0.108–0.216 mm·day^{-1} for twelve-month-old juveniles.

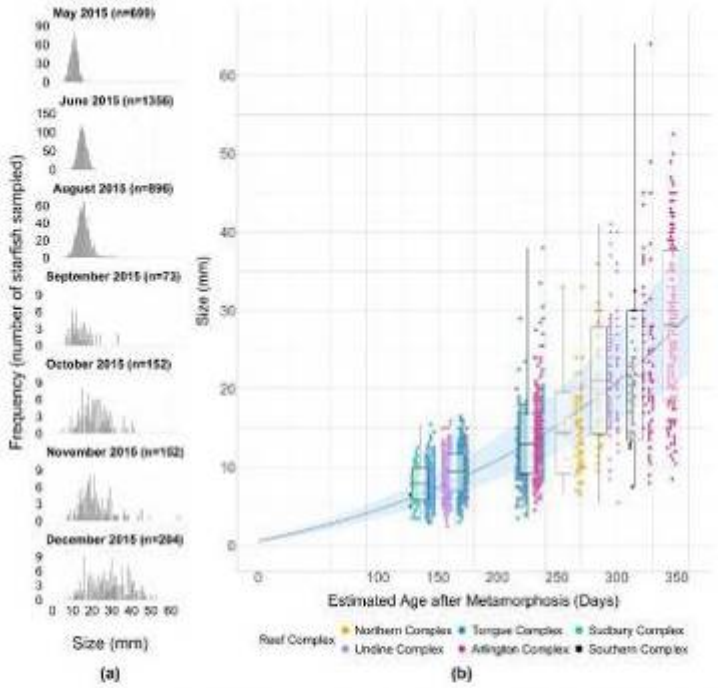

Figure 2. (**a**) Monthly size–frequency distributions of juvenile crown-of-thorns starfish sampled during May–December 2015; (**b**) Fitted growth curve ($m2_{Size\ at\ Age0=0.56}$, black line) and combined 95% confidence interval (light blue) for the 0+ year crown-of-thorns starfish cohort sampled in the northern Great Barrier Reef (GBR). The combined 95% confidence interval is formed by the lower and upper bounds of the 95% confidence interval of *m2* growth models with size at age 0 set to 0.30 mm and 0.82 mm, respectively. Individual starfish of the 2015 cohort are depicted as points, and the colours indicate the reef complex (see Figure 1). Each boxplot (by sampling month) is characterised by a mean size (horizontal middle line), ±one standard deviation (rectangle), and minimum and maximum size (vertical line). The vertical lines of the grid indicate 30-day intervals.

Table 1. Range of modelled mean sizes and growth rates for estimated age (in months after metamorphosis) and different time spans (30-day intervals).

Estimated Age after Metamorphosis (Months)	Time Span (30-Day Interval)	Range of Modelled Mean Sizes (mm)	Range of Modelled Growth Rates (mm·Day^{-1})
1	0–30	0.30–2.04	0.028–0.041
2	30–60	1.15–3.46	0.032–0.047
3	60–90	2.11–5.12	0.036–0.055
4	90–120	3.19–7.04	0.041–0.064
5	120–150	4.41–9.28	0.046–0.075
6	150–180	5.79–11.89	0.052–0.087
7	180–210	7.35–14.93	0.059–0.101
8	210–240	9.11–18.47	0.066–0.118
9	240–270	11.09–22.58	0.075–0.137
10	270–300	13.33–27.37	0.084–0.160
11	300–330	15.87–32.94	0.095–0.186
12	330–360	18.73–39.43	0.108–0.216

4. Discussion

This study provides the first estimates of monthly growth rates for 0+ year crown-of-thorns starfish on the GBR based on intensive field sampling of newly settled juvenile starfish. Juvenile crown-of-thorns starfish exhibited exponential growth over the first year on the reef and reached a size of up to 52.5 mm by mid-December. Size ranges of juveniles increased by a factor of 3.5 from May to December. The marked increase in size range was also reflected in the results of the growth curve analysis, which showed that the variation in size increased cubically with age in the best-fit models. Similarly, ranges of modelled growth rates increase with age; while one month old juveniles grow 0.028–0.041 mm·day^{-1}, twelve-month-old juveniles grow 0.108–0.216 mm·day^{-1}.

The increasing variation in size among older individuals may be attributed to variation in the availability of suitable coral prey within specific study sites and microhabitats. Although laboratory studies have shown that same-aged newly settled crown-of-thorns starfish vary in size from the beginning of their post-metamorphic life [23], marked variations in growth rates of juvenile starfish are generally attributed to the availability of suitable coral prey [20,38]. At settlement, crown-of-thorns starfish feed on coralline algae, and it is thought that they preferentially settle in locations (and microhabitats) where coralline algae are ubiquitous [18,39]. After an obligatory period of feeding on coralline algae (4.5—Yamaguchi 1973 [18]), juvenile starfish may or may not transition to feeding on Scleractinian corals, depending upon the local availability of suitable coral prey [10]. The fastest growth rates recorded in both field and laboratory settings are for individuals that make rapid transitions to coral feeding, resulting in accelerated growth and are reported to be significantly larger than siblings that continue to feed on algae [21]. Individual crown-of-thorns starfish that continue to feed on coralline algae after 4–5 months are thought to be more vulnerable to predation by epibenthic fauna [18], whereas fast-growing juveniles that make a rapid transition to feeding on coral—and thereby escape this predation pressure—are more likely to survive [40]. As sampling was conducted on 64 reefs across 111 sites, the availability of suitable coralline algae and coral prey would have differed considerably among microhabitats within and between sampling sites. Individual sampled starfish are likely to have been exposed to different environmental pressures (e.g., predation and food availability) in each of these microhabitats, which would have shaped their growth in the first year of development differently. Consequently, the gradual widening of the 95% confidence interval likely reflects differential growth rates between individuals that have transitioned to feeding on live coral versus those continuing to feed on coralline algae. This appears to be driven by a varying availability of suitable coral prey within microhabitats.

Ranges of modelled growth rates were broadly comparable to both laboratory-reared individuals released into the field [25] and the growth of juvenile cohorts in Japan and Fiji [10,17]. Observed mean sizes, standard deviations, and size ranges of juveniles sampled in these studies [10,17,25] were plotted to the fitted growth curve for comparison (Figure 3). Given the uncertainties related to the approach

taken to estimate age in Zann et al. (1987) [10] and Habe et al. (1989) [17], and the discrepancies related to ages being estimated in months instead of days, estimated ages were not standardised across different studies. Care should therefore be taken when interpreting the results of this comparison. While Zann et al. (1987) [10] and Habe et al. (1989) [17] followed distinct cohorts of juvenile starfish in the field, Okaji (1996) [25] deployed four groups of laboratory-reared juveniles of different ages (i.e., 2 × 0-, 2-, and 3-month old juveniles) for varying periods of time (i.e., 49, 37, 57, and 92 days, respectively). For each of these groups, he calculated an initial and final mean size before and after deployment in the field (Figure 3).

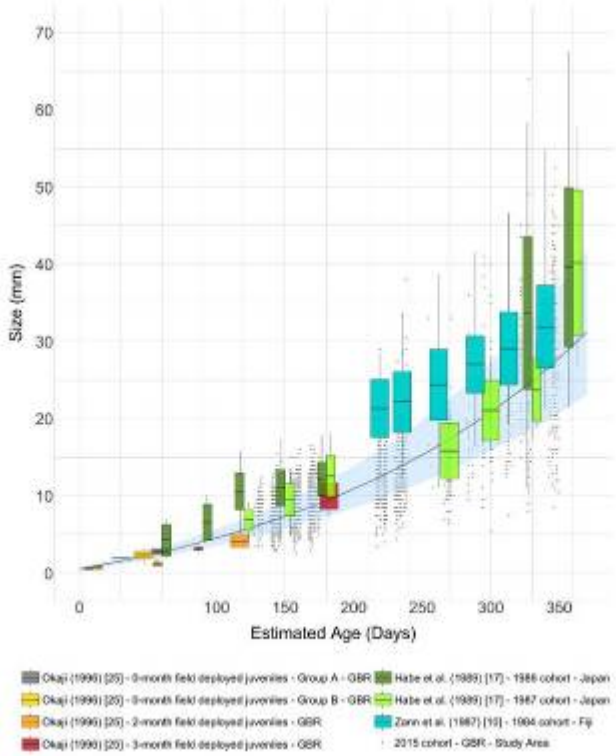

Figure 3. Fitted growth curve (black line) and combined 95% confidence interval for the 2015 crown-of-thorns starfish cohort (GBR). Individual observations of the 2015 cohort are depicted as points, while boxplots represent the results of previous field studies (Zann et al., 1987 [10], n = 651; Habe et al., 1989 [17], n_{1986} = 683 and n_{1987} = 125; Okaji, 1996 [25], $n_{initial}$ = 1137 and n_{final} = 138). Each boxplot is characterised by a mean size (horizontal middle line), ±one standard deviation (rectangle), and minimum and maximum size (vertical line). Note that the estimated age in Zann et al. (1987) [10] and Habe et al. (1989) [17] likely represents the age after fertilisation without taking into account potentially long planktonic larval durations (PLDs); ages are therefore likely to be underestimated. In contrast, the estimated age in Okaji (1996) [25] and the present study represents the age after metamorphosis (i.e., after settlement).

Ten-day old juveniles set out in the field on the GBR for 37–49 days grew on average 0.045–0.046 mm·day^{-1}, mostly within the range of the modelled growth rates for the same time span (i.e., 0.030–0.045 mm·day^{-1}) [25]. Similarly, growth rates for 2-month-old starfish

(deployment time = 57 days) averaged 0.053 mm·day^{-1} compared to 0.038–0.059 mm·day^{-1}; while 3-month-old starfish (deployment time = 92 days) grew at a rate of 0.074 mm·day^{-1} compared to 0.046–0.076 mm·day^{-1} [25]. Growth rates derived from the findings of field studies conducted in Fiji [10] and Japan [17] are also broadly comparable to the range of modelled growth rates of this study. In Fiji, growth rates averaged 0.087 mm·day^{-1} for juveniles between 7 and 12 months, largely falling within the modelled range of 0.073–0.135 mm·day^{-1}. Similarly, field studies conducted in Japan showed that juveniles (between 4 and 6 months old) from the 1986-cohort and 1987-cohort grew at 0.121 mm·day^{-1} and 0.139 mm·day^{-1} respectively, also within the modelled range of growth rates (i.e., 0.083–0.158 mm·day^{-1}) for the same time span. These results show that growth rates of juvenile *Acanthaster* spp. in the field appear to be remarkably consistent over large geographic scales. However, mean sizes of juveniles of the 1984-cohort (Fiji) and the 1986-cohort (Japan) deviate considerably from the modelled mean sizes (Figure 3). In both studies, age was estimated based on the date of spawning without taking into account of potentially long planktonic larval durations (i.e., up to 43 days [33]). For instance, juveniles that were sampled in Fiji in July were estimated to be seven months old, based on the assumption of a January spawning [10]. Similarly in Japan, newly settled starfish sampled in July were assumed to be one month old, based on the assumption of a mid-June spawning [17]. Assuming a mid-June spawning and a pelagic larval duration of two weeks, settlement would have occurred at the beginning of July at the earliest. However, juveniles that were collected in July and August were already 2 and 4.30 mm, respectively [17]. These sizes seem considerably large, as we know from laboratory studies that juveniles measure between 0.3 and 0.82 mm after settlement and that it takes approximately 40–45 days to grow to 2 mm, and 80–90 days to grow to 4.3 mm [18]. As a result, ages in Zann et al. (1987) [10] and Habe et al. (1989) [17] are likely to be underestimated by 0.5–1.5 months, resulting in overestimates of growth rates.

An implicit assumption of this study was that spawning occurred within a relatively limited period (in December 2014) across the entire study area. This assumption appears valid, given that the estimated growth rates for field-deployed juveniles of known age are broadly comparable to the range of modelled growth rates. The assumption of a single spawning event or narrow spawning window is also supported by the fact that smaller juveniles became rare as sampling progressed through the year (see Figure 2), indicating that settlement and so spawning did not occur throughout the entire year. Furthermore, spawning occurred in the study area between the 10 and 21 of December 2014 (temperature recorded at Lizard Island at 0.6 m between 12 and 30 December 2014: 28.58 °C–29.29 °C [41]) according to Uthicke et al. (2015) [28]. Assuming a planktonic larval phase of 10 to 40 days [22,23,29–31,33], settlement would have occurred between the 20 of December 2014 and 30 of January 2015. However, new research is suggesting that peak settlement likely occurs within 22 days after spawning and fertilization [33], and few larvae persist beyond 30 days post-fertilization. Accordingly, Uthicke et al. (2015) [28] failed to detect larvae in plankton samples from 13 of January onwards. If so, estimated ages (in days) of juveniles (measured from settlement) would have an accuracy of ±12 days.

Low ocean current velocities linked to El Niño-Southern Oscillation (ENSO) hydrodynamics that cause larval retention around reefs or within reef groups are thought to increase survival of crown-of-thorns starfish larvae when they co-occur with enhanced phytoplankton concentrations [42]. According to Wooldridge and Brodie (2015) [42], the 2009 spawning event—which led to the onset of the current outbreak in 2010/2011—coincided with nutrient-enriched stagnant shelf currents. Larvae of the studied cohort would have been present in the water column between 10 December 2014 and 13 January 2015 (temperature range recorded at Lizard Island weather station between 12 December 2014 and 15 January 2015: 27.9 °C–29.5 °C [41]). Mean phytoplankton concentrations (i.e., chlorophyll *a*) during this period averaged in the Wet Tropics 0.55 µg·L^{-1} (range: 0–7.35 µg·L^{-1}) for coastal areas, 0.31 µg·L^{-1} (range: 0.01–12.42 µg·L^{-1}) for midshelf areas, and 0.16 µg·L^{-1} (range: 0–8.09 µg·L^{-1}) for offshore areas [43]. In comparison, mean chlorophyll *a* concentrations in December 2009 averaged in the Wet Tropics 0.67 µg·L^{-1} (range: 0–11.61 µg·L^{-1}) for coastal areas,

0.31 $\mu g \cdot L^{-1}$ (range: 0.01–13.82 $\mu g \cdot L^{-1}$) for midshelf areas, and 0.19 $\mu g \cdot L^{-1}$ (range: 0–2.90 $\mu g \cdot L^{-1}$) for offshore areas [43]. While the Southern Oscillation Index (SOI)—which provides an indication of ocean current velocity (neutral SOI = surrogate for low shelf currents)—was −5.5 in December 2014 (compared to −7 in December 2009) and −7.8 in January 2015 (compared to −10.1 in January 2010) [43]. Subsequent SOI values continued to decrease in 2015 to a −20.2 low in October, indicating an El Niña event. Moderate increases in chlorophyll concentrations (up to 1.0–4.0 $\mu g \cdot L^{-1}$) that significantly increase rates of larval development, survival, and settlement [23,32,33] would have occurred on multiple occasions in the study area during the pelagic larval phase of the studied cohort. Consequently, larval development, survival, and settlement may have been enhanced in the study area during this time period, leading to high settlement rates and the development of this seemingly conspicuous cohort in 2015.

5. Conclusions

Demographic rates are fundamental to understanding population dynamics and creating meaningful population models. However, attempts to estimate these rates for 0+ year juvenile crown-of-thorns starfish have been hindered by the ability to detect them in the field [14–16]. The present study not only demonstrates that 0+ year juveniles can be sampled in high numbers (n = 3532), it also provides ranges of monthly growth rates to inform population models. Here, we also provide evidence that supports the assumption that spawning and subsequent settlement occurred in 2014–2015 during a relatively narrow period of time across a vast geographic area (i.e., 350 km) on the GBR. In addition, the predicted ranges of mean sizes for different sampling periods deliver valuable information to research and management bodies for the planning of juvenile monitoring studies. Rigorous ongoing monitoring should be conducted in the future on a number of selected sites to collect field-based data on demographic rates (e.g., growth, recruitment, mortality, and reproductive output rates) that can be related to variables such as food availability and adult population densities in order to inform population models and improve our understanding of population and outbreak dynamics.

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Conflicts of Interest: J.W. and D.S. provide marine consultancy services for crown-of-thorns starfish control and monitoring. They declare no conflict of interest.

Appendix A

Table A1. Mean sizes for newly-metamorphosed starfish reared in the laboratory under naturally occurring chlorophyll *a* concentrations [23].

Chlorophyll *a* ($\mu g \cdot L^{-1}$)	Mean Size (mm)	Standard Error (SE)	95% Confidence Interval (mm)
0.28	0.44	0.07	0.30–0.58
2.90	0.66	0.05	0.56–0.76
5.20	0.64	0.09	0.46–0.82

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Discussion

Forecasting marine invasions under climate change: Biotic interactions and demographic processes matter

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ABSTRACT

Biological invasions are one of the most significant threats to marine biodiversity, and can be facilitated and amplified by climate change. Among all aspects of invasion biology, biotic interactions between invaders and native species are of particular importance. They strongly influence the invasion velocity as well as species responses to climate-induced stressors. Yet the effects of biotic interactions and other important demographic processes remain overlooked among most studies of climate-mediated invasions. We critically assessed current modelling techniques for forecasting marine invasions under climate change, with a particular focus on their ability to account for important biotic interactions and demographic processes. We show that coupled range dynamics models currently represent the most comprehensive and promising approach for modelling and managing marine invasions under climate change. We show, using the crown-of-thorns seastar (*Acanthaster planci*), why model architectures that account for biotic interactions and demographic and spatial processes (and their interaction) are required to provide ecologically realistic predictions of the distribution and abundance of invader species, both under present-day conditions and into the future. We suggest potential solutions to inform data-poor situations, such as Bayesian parameter estimation and meta-analysis, and identify strategic and targeted gaps in marine invasion research.

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1. Introduction

Marine invasive species are a major threat to biodiversity worldwide and can have profound ecological and economic impacts on marine ecosystems (Bax et al., 2003). Although the criteria that categorise a species as invasive remain somewhat controversial, invaders are commonly characterised as species that undergo rapid increases in abundance and/or spatial occupancy with adverse effects on recipient ecosystems (Valery et al., 2008). This definition includes the case of 'native invaders' that can spread within their historical range by exploiting niche opportunities resulting from human activities and/or loss of other species: by attaining extreme abundances and exerting severe per-capita effects on local communities, native invaders can indeed cause ecological impacts that rival those of non-native invaders (Valery et al., 2009; Carey et al., 2012). Whether native or not, invaders can impact recipient communities directly through competition, predation, and hybridization, and indirectly by modifying habitats and potentially disrupting their suitability. Over 1500 species have invaded locations throughout the world's oceans, and more are discovered every year (European Environment Agency, 2012). The potential economic costs incurred by even a single marine invasive species can reach US$250 million yr^{-1} (Williams & Grosholz, 2008) and eradication seems possible only in highly constrained situations (Bax et al., 2002). Future climate change is predicted to increase the introduction and spread of invasive species, accelerating marine invasions and resulting in widespread biodiversity loss (Garcia Molinos et al., 2016).

The ecological traits that commonly characterize marine invasive species are disproportionately favoured under climate change, potentially exacerbating future impacts of marine invasions (Poloczanska et al., 2013). This is because marine invaders often tend to be generalist and/or opportunists with relatively plastic life histories (Clavel et al.,

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2011), making them able to better adapt to rapidly changing environmental conditions and fare better in warming waters than native species (Sorte et al., 2013; Bates et al., 2013). By relaxing some of the physiological constraints on temperature-dependent growth and survival while also altering connectivity, human-induced climate change has already enabled some non-native invasive species to expand into regions where they previously could not survive and reproduce, as exemplified by the green 'killer' algae *Caulerpa taxifolia* in the Mediterranean (Walther et al., 2009). Additional climate-related factors that might enhance a species' invasive ability include: extensions of spawning periods and increases in per capita reproductive output (Walther et al., 2009); altered timing of recruitment and faster growth in warmer years (Stachowicz et al., 2002); faster developmental rates (Walther et al., 2009); and modified local dispersal patterns due to altered hydrodynamic conditions (Diez et al., 2012). In the case of native invaders, climate-driven environmental changes at local scales (e.g. eutrophication, altered connectivity due to changes in ocean currents) can favour the dominance of invaders in parts of their historical range where they previously could not survive or reproduce (Carey et al., 2012).

Despite these established physiological and demographic responses to climate change, there have been few attempts to forecast the potential impact of invasive species under climate change and test the efficacy of alternative management actions (Sorte, 2014). Most existing knowledge is based on local field observations or mesocosm experiments (e.g., Cockrell & Sorte, 2013) that are often conducted at small scales and/or do not necessarily represent realistic environmental conditions. More integrated approaches that combine empirical data on local and regional ecological processes with simulation models are urgently needed in marine invasion biology to improve our knowledge of impending invasions and to manage existing and future invasive species (Fordham, 2015).

A commonly overlooked consequence of climate change affecting marine invasions is the way climate change alters ecological interactions in native communities (Sorte et al., 2010). Climate-driven changes in invasive ability affect the way native communities are organised, facilitating the formation of novel ecological communities characterised by new arrangements and ecological interactions (Lurgi et al., 2012). Such new configurations can create ecological vacuums that facilitate future invasions, especially if top predators are depleted (as frequently reported in response to global change; Cheung et al., 2015). Other anthropogenic stressors such as fisheries exploitation, terrestrial runoff, and eutrophication can act in synergy with climate change to facilitate not only invasions by alien species but also state-shifts of species dominance, as for example, in the case of invasive jellyfish (gelatinous plankton; Fig. 1) (Licandro et al., 2010; Lynam et al., 2011). These interactions can be complex, with climate change and other anthropogenic stressors having both direct and indirect effects on the strength of biotic interactions (e.g. competition, predation). Consequently, not only is the dominance of invasive species likely to change owing to synergies between anthropogenic stressors, but also the number and strength of their biotic interactions between invasive and other species, with potentially multiplying effects brought about by trophic cascades (Lynam et al., 2011).

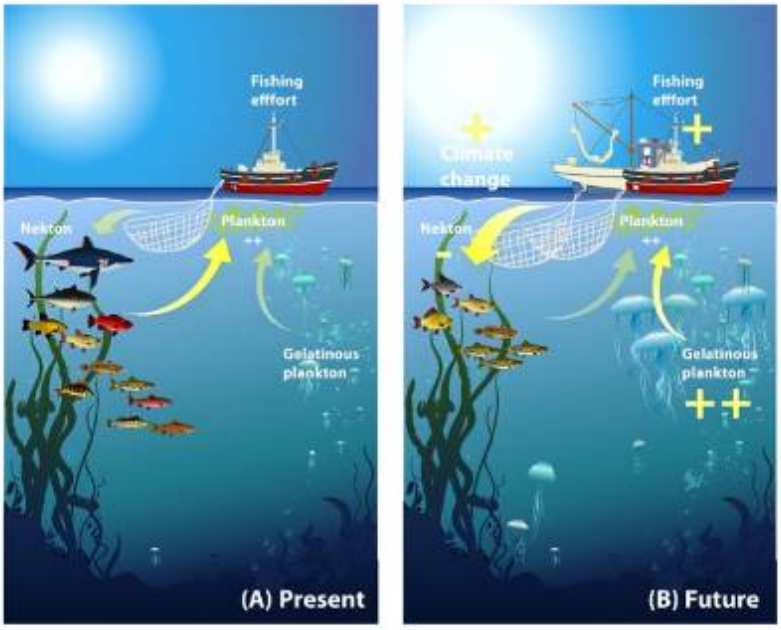


Fig. 1. One conceptual model of mutually reinforcing effects of climate change and other anthropogenic stressors on native invasive jellyfish (gelatinous plankton), with biotic interactions (i.e., predator-prey relationships) represented by the arrows. (**A**) Increasing terrestrial runoff and nutrients loads contribute to eutrophication, leading to unusually high phytoplankton (*plankton*) concentrations associated with low oxygen concentrations (Miller & Graham, 2012). These conditions promote the growth of jellyfish populations, sustained by plankton resources usually consumed by fish stocks and fish larvae (*nekton*). Fish stocks are subsequently impacted by this reduced availability of plankton resources, as well as by continuously increasing *fishing effort* (e.g. Pauly et al., 2002). The reduced size of fish stocks results in a reduced uptake of planktonic resources, thus made available to sustain further jellyfish blooms (Licandro et al., 2010; Lynam et al., 2011). (**B**) *Climate change* favours gelatinous plankton species that are able to adapt to new environmental conditions and increase in abundance rapidly (Lynam et al., 2011). The composition of nekton communities and fish stocks is altered not only as increasing fishing efforts remove fish predators (Pauly et al., 2002) but also as surface temperature increases leading to the dominance of (sub)tropical species (Cheung et al., 2013). Because these subtropical species are unlikely to prey on the same plankton species as their temperate peers, planktonic resources not consumed by fish are more readily available to sustain increasingly frequent and extensive jellyfish blooms.

Anticipating and managing future threats from invasive species to marine biodiversity thus requires accurate forecasts of marine invasions that account for biotic interactions between native and invasive species, and how they are likely to change in response to multiple anthropogenic stressors. Here we appraise the quantitative methods that have been applied to forecast marine invasions, focusing on their strengths and shortcomings, and on whether they can explicitly account for biotic interactions. We then implement a spatially explicit simulation model as a proof-of-concept of how biotic interactions, demographic processes and their climate-induced variation can and should be integrated into forecasts of marine invasions under climate change. Our model organism is *Acanthaster planci*, the crown-of-thorns seastar, which is a major threat to the Great Barrier Reef, and the only threatening process of contemporary global change that is amenable to direct management actions (De'Ath et al., 2012). Rapid outbreaks of *A. planci* currently pose one of the most serious management problems for the Great Barrier Reef, leading to conservation implications (e.g., extirpation of foundation species and destruction of essential fish habitats) that are similar to those of any non-native invasive species.

2. Recent developments for forecasting marine invasions under climate change

2.1. Species distribution models

Correlative species distribution models (SDMs; i.e. ecological niche, bioclimatic envelope, or habitat suitability models) describe or predict the probability of presence or spatial abundance of a species across environmental gradients or in a specific geographical area based on habitat suitability (Pearman et al., 2008). SDMs have very simple data requirements, needing only point location data and associated environmental variables (Table 1). However, predictions are often constrained by important limiting assumptions (Elith et al., 2010; Robinson et al., 2011). Indeed, SDMs typically assume that species occurrences represent the range of environmental conditions in which an organism can persist (Schurr et al., 2012) and rarely account for demographic processes such as dispersal in an ecologically realistic way (Travis et al., 2013). These assumptions are particularly concerning in the case of recently introduced invasive species because their ranges are by definition expanding (e.g., Kearney et al., 2008), thus representing a non-equilibrium distribution (Thuiller et al., 2005). As a result, models calibrated in the native range often underperform in the exotic range (and vice versa) (Fitzpatrick et al., 2007), an issue that can be partially addressed by considering the species' global range (Mainali et al., 2015).

The failure of SDMs to account explicitly for biotic interactions (as well as demographic processes) has been identified as a major limitation of these models, affecting predictions of distributional shifts under changing climatic conditions (Araujo & Luoto, 2007). While biotic interactions can keep a species in check in climatically suitable conditions, they can also fail to restrict invasions in new territories where a predator or competitor is absent or in low abundance (Fig. 1) (Mainali et al., 2015). In such a situation, SDMs unrealistically consider the invaded range as climactically broader than the native range (e.g., Fitzpatrick et al., 2007). Recognition of these limitations has prompted the development of new methods for incorporating biotic interactions into SDMs (Kissling et al., 2012). These methods include: (*i*) adding the occurrence of an interacting species as an additional covariate in the SDMs (Araujo & Luoto, 2007); (*ii*) developing a separate SDM for the interacting species and using it to constrain the distribution of the focal species, minimizing the issues of false absences and collinearity where both species are related to the same environmental predictors (Schweiger et al., 2008); or (*iii*) calibrating an interaction matrix among species to define the error matrix for multivariate logistic regression models (Kissling et al., 2012).

Existing methods for incorporating biotic interactions into SDMs remain problematic for at least two reasons: biotic interactions can

Table 1
Modelling techniques currently available for forecasting marine invasions under climate change: data requirements, ecological processes captured, and examples of previous application.

Model designation	Data requirements					Processes accounted for				Marine examples
	Occurrence	Abundance/ density	Environmental data	Physiological data	Demographic data	Dispersal	Individual behaviour	Predator prey	Larval connectivity	
SDM	✓	✓	✓						Species-environment relationships	(de Rivera et al., 2011) (Tyberghein et al., 2012) (Jones et al., 2013)
Biophysical models			✓	✓					Physiological tolerance	(Fordham et al., 2013b) (Cheung et al., 2015)
Population-based demographic models	✓	✓	✓	✓	✓	✓			Growth, survival, dispersal	(Dunstan & Bax, 2007) (Cheung et al., 2011) (Cocker & Sorte, 2013) (Fordham et al., 2013b)
Individually-based demographic models	✓		✓	✓	✓	✓	✓	✓	Reproduction, aggregation, behaviour	(Rijnsdorp et al., 2009) (Anderson et al., 2013)

change over time (even more so in the context of an invasive species under climate change; Fig. 1) and it is difficult to include more than one interaction at a time. Therefore, biotic interactions remain absent from most SDMs under the assumption that, at least at biogeographic scales (as opposed to local; Wisz et al., 2013), biotic interactions are not a determinant of invasive species distributions (Mainali et al., 2015), which seems unrealistic in most situations (Araujo & Luoto, 2007). Recent studies using SDMs to forecast marine invasions have focused primarily on the susceptibility of environments to invasions for management purposes (de Rivera et al., 2011; Jones et al., 2013). Biotic interactions have, however, been consistently ignored in these marine SDMs (Robinson et al., 2011).

2.2. Biophysical models

Biophysical models (i.e. process-based models) rely on species physiological tolerance limits and, in doing so, enable species distributions to be modelled across environmental gradients without using occurrence data (Kearney et al., 2008) (Table 1). Biophysical models should, in theory, yield more robust forecasts of climate-driven distributional shifts because they explicitly account for relationships between climate conditions and organismal performance. In doing so, biophysical models overcome problems associated with non-equilibrium situations, since they do not rely on occurrence data that could misrepresent the species' potential range due to biotic interactions (see above) or human-driven impacts such as depletion from harvesting (Buckley et al., 2010). Biophysical models are increasingly used to model range dynamics in response to climate change (Kearney et al., 2008; Cheung et al., 2011) or environmental gradients (Monahan, 2009), and can be coupled with SDMs to constrain their predictions (Elith et al., 2010; Buckley et al., 2011; Fordham et al., 2013b). For example, biophysical models have been used to show that invasion of the Indo Pacific lionfish (*Pterois volitans*) into the Mediterranean is unlikely to occur due to low connectivity between suitable sites (Johnston & Purkis, 2014). Biophysical models subsequently allowed to recreate the success/failure of invasions of introduced fish in the Hawaiian Islands, providing insight into the demographic properties that predispose fish species to successful invasion (Johnston & Purkis, 2016). Biotic interactions cannot currently be implemented in biophysical models in their original form but would represent an important and desirable extension to this class of models (Buckley et al., 2010; but see Tingley et al., 2014).

2.3. Spatially explicit demographic models

Spatially explicit demographic models, which directly account for species vital rates in model predictions, are used with increasing frequency to model the effects of climate change on the range dynamics and persistence of species, including those in the marine realm (e.g., Fordham et al., 2013b). While incorporating important information on habitat suitability (e.g., Mellin et al., 2012), such models relax some of the limiting assumptions constraining SDMs since they explicitly account for dispersal and source-sink dynamics, enabling demographic rates (such as growth or fertility) to vary in space and time (Dunstan & Bax, 2007). Models can be either population-based (i.e. they account for population-level parameters such as survival and fertility rates, dispersal kernels) or individual-based (e.g. incorporating individual heterogeneity in parameters such as body size, movement and feeding behaviour, phenotype). For both population- and individual-based demographic models, user-friendly and fully customisable modelling platforms are now broadly available (Lurgi et al., 2015) (Table 1). Most recently, some of these frameworks have been adapted to explicitly account for simple (one-way) biotic interactions in predictions of how climate change is likely to affect species range dynamics (e.g., Fordham et al., 2013a).

In spite of readily available modelling platforms, and available demographic data for some species, marine applications of spatially explicit demographic models for invasive species remain scarce. Demographic (stage-structured) models have for example been used to predict the future population growth of invasive species using laboratory mesocosms to estimate survival, growth, and fecundity rates within epibenthic communities under present-day conditions and with ocean warming (Cockrell & Sorte, 2013). This approach is informative in situations where the population dynamics of local communities are explained mainly by intrinsic demographic properties of the constituent species. Demographic models have also been used to understand how range dynamics can be affected by environmental changes and to forecast potential effects on abundance and geographic distributions. For example, commercial fisheries researchers now use hybrid demographic models (named Dynamic Bioclimate Envelope Model), which explicitly account for demographic and range dynamics (Cheung et al., 2009; Cheung et al., 2011), to incorporate competition for resources into predictions of species distributional shifts (Fernandes et al., 2013). Forecast latitudinal shifts decreased by 20% when species interactions were considered, further highlighting the importance of biotic interactions in forecasting distributional shifts and marine invasions.

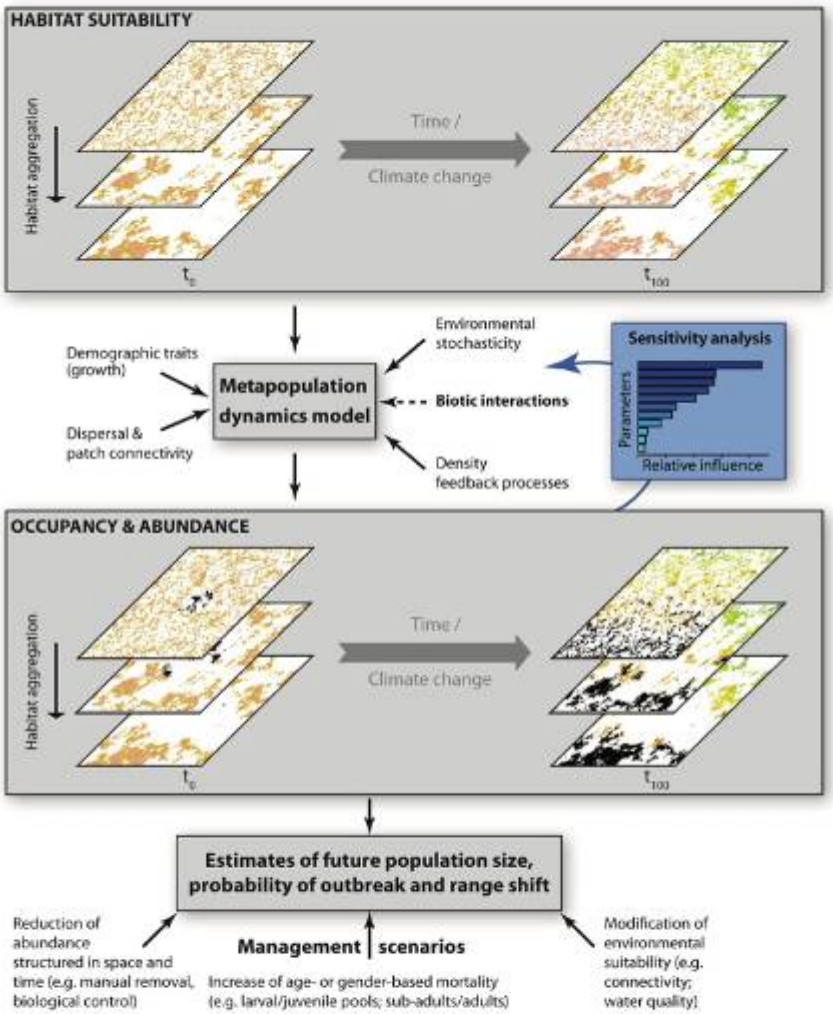
In aggregate, if we are to better forecast marine biological invasions and understand their effects on recipient communities, there needs to be a much stronger focus on developing quantitative approaches that account for key ecological processes (demography and biotic interactions) in simulation models of marine invasions. Coupled range dynamics models, accounting for metapopulation processes and simulating the mutually reinforcing effects of climate change and biotic interactions (Fig. 1), provide appropriate modelling frameworks that have not yet been used to simulate marine invasions. This is despite the necessary tools being widely accessible, and similar methodologies having been developed for modelling species range dynamics under climate change in terrestrial ecosystems (both aspects reviewed by Lurgi et al., 2015) including invasive terrestrial species (Fordham et al., 2012) and harvested marine species (Fordham et al., 2013b). The demonstrated utility of this approach indicates the immediate need for an assessment of its transferability to the case of marine invasions.

3. Incorporating biotic interactions into forecasts of marine invasions

To demonstrate the feasibility of coupling demographic models with SDMs (i.e. coupled range dynamics models) in order to forecast spatially explicit changes in the range and abundance of marine invasive species, we developed a population-based cellular automaton (Durrett & Levin, 1994). We use this coupled range dynamics model to show (*i*) how biotic interactions can be incorporated into forecasts of invasion dynamics under climate change and (*ii*) the extent to which doing so influences model outcomes and potential management applications (Box 1; see Supplementary material SM1 for a full description of the framework). We chose the coral-eating crown-of-thorns seastar (*A. planci*) as a model organism. Outbreaks of *A. planci* have been a major contributor to the loss of half of the coral cover on Australia's Great Barrier Reef since 1985 (De'Ath et al., 2012). It was suggested that the frequency of such outbreaks has increased over the last century, partly as a result of increasing terrestrial runoff and primary productivity that promotes larval survival (Fabricius et al., 2010). Since *A. planci* can become sporadically hyperabundant in its native range, threatening the regional persistence of many corals and causing as much ecological damage as any non-native invasive species, it makes an interesting 'proof-of-concept' case study for modelling (and managing) marine invasions under climate change.

We considered two different model-based scenarios: a trophic interaction between *A. planci* and its coral prey (*Scenario I*) vs. no biotic interactions (*Scenario II*). We then developed three artificial seascapes reflecting increasing levels of habitat clustering (from evenly distributed to highly aggregated suitable habitat) to gauge the potential effect of patch structure (and corresponding connectivity) on the population

Box 1
Simulation model.



Conceptual representation of the population model. Habitat suitability across the seascape (layers) ranges from low (green) to high (pink). White cells are unsuitable and occupied cells are shown in black.

We constructed a population-based cellular automaton (Durrett & Levin, 1994) model for the crown-of-thorns seastar (*Acanthaster planci*) that simulated population and range dynamics under climate change according to two scenarios: dispersal + population growth + biotic interactions (*Scenario I*) and dispersal + population growth (*Scenario II*). Essential aspects of the model can be summarised as follows (see Supplementary material for full model description and implementation details):

- ***Habitat suitability***: defined based on 2D simulated seascapes characterised by variable levels of clustering (i.e. aggregation) from numerous small patches (cluster 1) to a few large patches (cluster 3). The distribution of habitat suitability values across grid cells was kept constant among clustering levels. The resulting maps carry information on habitat suitability, which in turn determines the carrying capacity.
- ***Simulating the effects of climate change***: This was achieved by altering dynamically the potential climate suitability of each local unit of the

meta-population (grid cell) at each iteration of the model, and combining it with the original habitat suitability layer. The temporal change in habitat suitability across the seascape reflected a southerly range shift commonly observed in conjunction with latitudinal range dynamics (Parmesan, 2006), with northernmost habitats becoming progressively unsuitable and southernmost habitats becoming more so.

- ***Demographic traits***: We modelled fertility, survival, dispersal and population growth. Survival and fecundity varied spatiotemporally in response to environmental variability (see below).
- ***Local populations connectivity via dispersal processes***: We allowed propagules (i.e. pelagic larvae) of the invasive species and its interacting prey species (*Scenario I* only) to disperse across the seascape. We defined dispersal from local populations based on a dispersal kernel and individual-level probabilities of dispersal. Adults were considered sessile.
- ***Environmental stochasticity*** accounted for stochastic variation in population growth rates.
- ***Biotic interactions***: Predator-prey interactions between *A. planci* and a generic coral prey species were simulated using Lotka-Volterra (predator-prey) equations (*Scenario I* only).
- ***Density dependent processes*** were modelled by allowing population density to increase up to the carrying capacity, after which individuals die and density returns to non-outbreaking levels.

We ran 100 simulations of 120 time steps each, discarding the first 20, which were used as the burn-in period. We summarised the outputs across simulations in terms of abundance and occupancy of the invasive species and its coral prey (*Scenario I* only). We ran a sensitivity analysis with the main model parameters varying between ± 20% over a total of 200 models as determined by Latin hypercube sampling, and then used boosted regression trees to determine the most important parameters (Supplementary material).

dynamics and distribution of *A. planci*. Climate change was simulated based on a latitudinal change in potential climate suitability, with the southernmost habitats becoming more suitable and northernmost habitats becoming less so over the 100-year time period considered (Lamare et al., 2014). Finally, we accounted for demographic traits and processes including fertility, dispersal, population growth, and density-dependent survival (e.g., accounting for the fact that individuals die and populations are reduced to non-outbreaking sizes once they reach a critical density threshold; Pratchett, 2005) (Box 1 and Supplementary material).

Ecologically realistic fluctuations in total population size mirrored the outbreaking dynamics observed on the Great Barrier Reef (Fabricius et al., 2010) only when biotic interactions were explicitly modelled (*Scenario I*; Fig. 2A). Occupancy patterns were characterised by temporal fluctuations that reflected lagged changes in the spatial distribution of prey abundance (Fig. 2A bottom panel). In contrast, in the scenario without biotic interactions (*Scenario II*), we show a steady decline in the total occupied range area and total population abundance of the invasive species over time (Fig. 2B). The effects of habitat clustering were more pronounced when no biotic interactions were considered (differences among rows in Fig. 2B). More clustered aggregations of suitable habitat generated smoother changes in population dynamics as habitat suitability shifted in response to climate change. The mechanism behind this is a greater connectivity among local populations within highly clustered habitats, which facilitates synchronisation among populations, homogenising the response to climate change. In Scenario I, this greater level of connectivity in highly clustered habitats also caused higher outbreak population sizes of *A. planci*. Moreover, climate change only affected occupancy patterns in Scenario I, with the average spatial extent an outbreak (i.e. number of occupied cells at each peak) decreasing over the 100 year period (Fig. 2A bottom panel). Conversely, there was no evidence of decrease in the size of the outbreaking population over time (Fig. 2A top panel).

4. Forecasting and managing marine invasions under climate change

Previous research has started to unravel the importance of accounting for population dynamics when trying to forecast range shifts and changes in abundance (Keith et al., 2008; Fordham et al., 2013b). A more recent, critical consideration is how to incorporate intra- and inter-specific biotic interactions into forecasts of future trends in abundance and geographical range limits under climate change (Fig. 1). Such biotic interactions can strongly influence the effect of climate change on marine invasions, sometimes even reversing the direction of species-specific responses to a particular stressor (when a species is affected by a stressor only in the presence or absence of another species) (e.g., Teng & Apperson, 2000). If we are to fully understand and better forecast marine invasions, we need coupled range dynamics models that are able to incorporate the most relevant aspects of species-level biology and ecology, along with their major interactions. Our coupled range dynamics model for *A. planci* builds upon recent and flexible platforms for modelling single-species invasions (e.g., Savage & Renton, 2014), providing a proof-of-concept that, for this simple system, direct biotic interactions can be integrated into forecasts of marine invasions under climate change with relative ease. Notably, our "proof-of-concept" modelling exercise demonstrates that accounting for simple prey-predator interactions strongly influences forecasts of range movement and population abundance; and that real-world population trends (i.e., those observed on the Great Barrier Reef) can only be reproduced using simulations that account explicitly for biotic interactions. Our findings highlight the importance of identifying the most important sources of environmental and biotic interactions and then integrating them with an appropriately scaled spatially explicit demographic model to forecast invasions under climate change.

Our modelling framework provides a generic tool that can readily be applied to any other marine pest (see Python code in Supplementary material) where data is available for model parameterisation. Its flexibility allows to incorporate variable biotic interactions under climate change, as well as the impact of thermal or other stress on demographic rates (e.g., decreased fertility; Fordham et al., 2013b). Nonetheless, we suggest that only the most pertinent biotic interactions should be included, based on expert knowledge, published literature, meta-analysis or experimentation. This is because not all aspects of ecosystems can or should be accounted for in model projections since doing so will result in over-parametrized models that are computationally unwieldy and difficult to validate or duplicate (Grimm et al., 2005; Fulton et al., 2015). Finally, it is worth noting that the specificities and constraints particular to the model we developed for *A. planci* can be easily relaxed to capture different processes and mechanisms affecting corals, such as bleaching and cyclones. Including recent data-driven observations of coral impact and recovery following disturbance (Mellin et al., 2016) in the model is a key next step forward.

Arguably, tight integration of the ecological processes considered above into a comprehensive modelling framework for marine invasions can be dauntingly complex and prohibitively challenging, partly because of the difficulties in collecting the data needed to parameterise such models. However, there are solutions. Plausible parameter estimation can be achieved using approximate Bayesian computation (Beaumont, 2010) or the elicitation of expert knowledge (Martin et

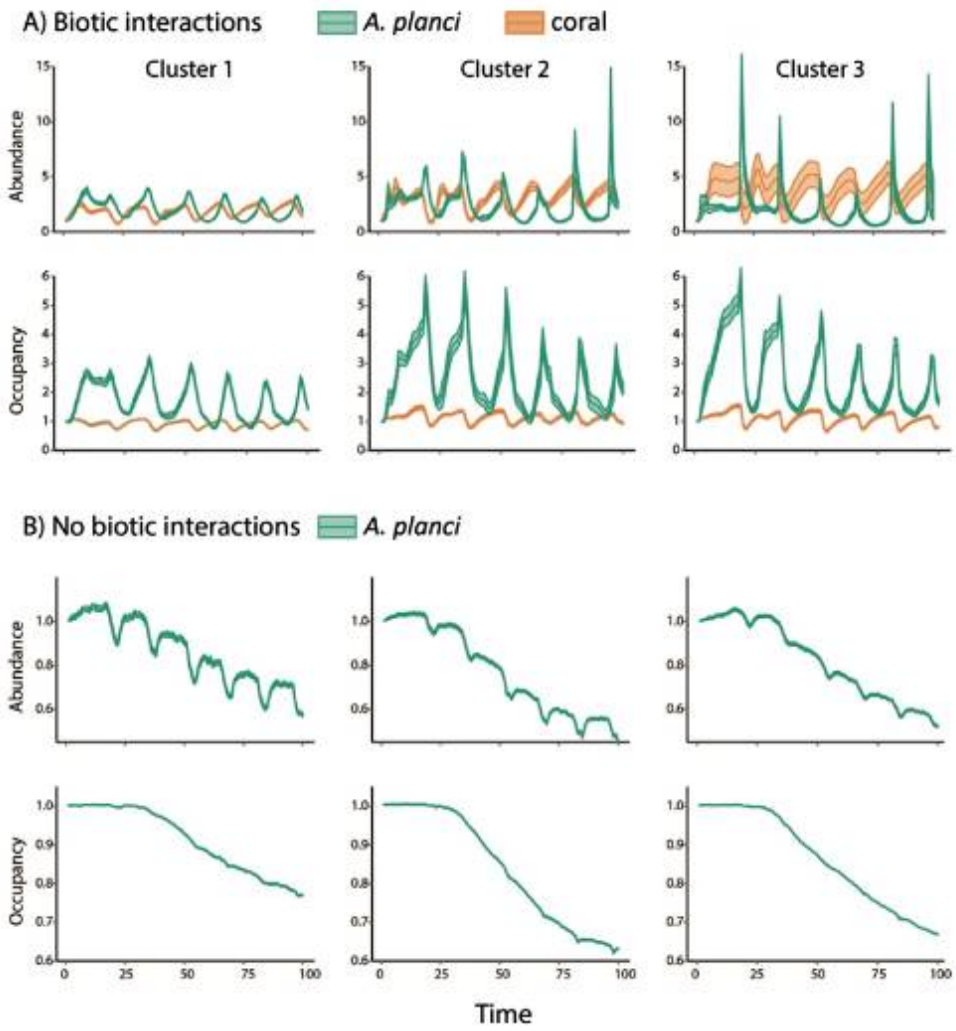


Fig. 2. Forecasts of a marine invasion process under climate change using a spatially explicit demographic modelling framework. Model parametrisation is based on a synthetic example for the coral-eating crown-of-thorns seastar (*Acanthaster planci*) and its coral prey (see text). (*A*) *Scenario I* includes a trophic interaction between the marine invasive species and its coral prey, while (*B*) *Scenario II* considers only dispersal and population growth. In both panels (A, B), top and bottom rows show population size and spatial occupancy over time, respectively; columns represent levels of clustering (i.e. aggregation) in suitable habitat from cluster 1 (numerous small patches) to cluster 3 (few large patches). Climate change was modelled using variable habitat suitability layer from time step 1 to 100 (the length of simulations). See Supplementary material for a detailed description of the model implementation.

al., 2005). Model parameters can then be calibrated by comparing model predictions with independent observations (Wells et al., 2015). Indeed, not all model parameters will have a significant effect on model outcomes, and sensitivity analysis (McCarthy et al., 1995) can help determine where future research efforts should be focused to improve model parameters and subsequent predictions. In the case of *A. planci* for example, our sensitivity analysis showed that natural mortality rate was the most important determinant of population size and occupancy (Suppplementary material). Since natural mortality is typically difficult to quantify (Pratchett et al., 2014), estimates are somewhat uncertain and future research efforts should therefore focus on improving such estimates of mortality. Second, while it is crucial to consider stressors other than temperature and the potential interactions among them, there remain significant gaps in our understanding of responses to such stressors, as well as how species-specific responses will propagate at the community level (Sorte, 2014). This is where meta-analyses can provide invaluable sources of information on how an organism might respond to a given stressor based on the taxon, life stage, habitat, and potential interactions with other stressors (e.g., Przeslawski et al., 2015). Meta-analyses can also help define the strength and direction of interactions among stressors in an integrative model, irrespective of divergences in defining the type of interactions

considered (i.e. synergistic, antagonistic, and additive effects) (Piggott et al., 2015).

Two critical post-hoc steps will determine the successful uptake of model outcomes by stakeholders, namely (*i*) model validation and (*ii*) quantification of uncertainty through each step of the model. Demographic models are typically validated by hindcasting abundance over the period for which independent observations are available, and comparing model predictions with observations (Wells et al., 2015). Ideally, in the most data-rich situations, validation can also be done using genetic estimates of population relatedness and source-sink dynamics (Fordham et al., 2014). Uncertainty on the other hand, is a neglected issue that can be complex to address. Attempts have been made to quantify data-related (observational or aleatory) vs. model-based (epistemic) uncertainty (Fordham et al., 2013c), and software developed to allow uncertainty in model parameters (and their interactions) to propagate through to model outputs and influence decision-making (Fordham et al., 2016).

The framework described here can and should be used to examine and rank the efficacy of alternative control strategies (in space and time) including: actively removing the invader; altering habitat suitability (e.g., through predator protection in no-take areas); and managing key dispersal corridors for the invasive species or its predators. The approach can also be used address whether management effort should focus on controlling the centre (source) of a population or the spreading periphery (Williams & Grosholz, 2008) under climate change. Due to epistemic uncertainty, forecasts of any invasion should be considered with caution, and it will often be more desirable to focus on differences among scenarios rather than on specific forecasts per se. In this way, the benefit of a particular management action should be measured against its counterfactual, i.e. what would happen if resources were spent on an alternative control option (Wilson et al., 2006), to provide a more sound basis for decision making than individual forecasting.

5. Conclusion

During recent decades, invaluable knowledge has been gained about the mechanisms and consequences of biological invasions in warming oceans, and there is now a need to shift attention from the properties of invading organisms to forecasting invasions in a changing world. Our methodology begins this task by building on previous modelling efforts to incorporate range dynamics, demography, and biotic interactions. Importantly, methodologies exist to tackle data limitation issues (e.g. Bayesian parameter estimation, meta-analysis, expert elicitation), making demographic model development tractable as part of an adaptive learning process. We suggest that strategic pathways should be developed to inform model inputs, interactions among stressors and their inherent uncertainty- the successful integration of which will determine model uptake and benefits in terms of conservation. Finally we emphasize the importance of validating model predictions and interpreting model results in a way that reduces the effects of epistemic uncertainty.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.biocon.2016.11.008.

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Water quality mediates resilience on the Great Barrier Reef

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Threats from climate change and other human pressures have led to widespread concern for the future of Australia's Great Barrier Reef (GBR). Resilience of GBR reefs will be determined by their ability to resist disturbances and to recover from coral loss, generating intense interest in management actions that can moderate these processes. Here we quantify the effect of environmental and human drivers on the resilience of southern and central GBR reefs over the past two decades. Using a composite water quality index, we find that while reefs exposed to poor water quality are more resistant to coral bleaching, they recover from disturbance more slowly and are more susceptible to outbreaks of crown-of-thorns starfish and coral disease—with a net negative impact on recovery and long-term hard coral cover. Given these conditions, we find that 6–17% improvement in water quality will be necessary to bring recovery rates in line with projected increases in coral bleaching among contemporary inshore and mid-shelf reefs. However, such reductions are unlikely to buffer projected bleaching effects among outer-shelf GBR reefs dominated by fast-growing, thermally sensitive corals, demonstrating practical limits to local management of the GBR against the effects of global warming.

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